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Long-Term Change in Copepod Community Structure in the Western Antarctic Peninsula: Linkage to Climate and Implications for Carbon Cycling

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LONG-TERM CHANGE IN COPEPOD COMMUNITY STRUCTURE IN THE WESTERN ANTARCTIC PENINSULA: LINKAGE TO CLIMATE AND IMPLICATIONS FOR CARBON CYCLING

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ABSTRACT

Copepods are the dominant mesozooplankton in the Southern Ocean, but long-term change in their abundance and distribution along the Western Antarctic Peninsula (WAP), a region experiencing rapid climate warming, is unknown. Copepods are also potentially important grazers of phytoplankton in the WAP and contributors to carbon export through production of sinking fecal pellets. I examined summer (January-February) copepod community structure and abundance along the WAP over two decades (1993-2013) and investigated long-term trends in copepod abundance and their relationship with environmental parameters (sea ice, phytoplankton biomass and productivity, climate indices, and sea surface temperature). Copepods comprised on average 81% of total mesozooplankton abundance in the WAP; the copepod community was dominated by a few species that included *Metridia gerlachei*, *Oithona* spp., and *Calanoides acutus*. There was a significant long-term increase in total copepod abundance over time, with higher abundances in years with earlier sea ice retreat and higher phytoplankton biomass and productivity. Trends for individual species reflected feeding and life cycle strategies, but generally followed those of total copepods. To examine the impact of copepod grazing on phytoplankton and contribution to carbon export, I conducted grazing and fecal pellet production experiments with the large dominant copepods (*Calanus propinquus*, *Rhincalanus gigas*, and *C. acutus*) in the WAP each January from 2012 to 2014. Copepods have a low overall impact on grazing of phytoplankton biomass (<1%) and productivity (1%, up to 11%). Copepods were likely feeding on other sources of carbon (i.e., protozoans and metazoans) besides phytoplankton to meet metabolic demands, especially in the offshore, slope region and in low chlorophyll *a* conditions. Fecal pellet production (egestion) rates were high, ranging from 0.82 (*R. gigas)* to 37.3_μC ind. day^{-1} (*Paraeuchaeta antarctica)*, and did not exhibit regional trends. My results suggest mechanisms leading to interannual variability of summer copepod abundance and grazing in the WAP can be used to predict how copepods will respond to future environmental changes and may affect the flow of carbon through the food web and the export of carbon to depth.

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CHAPTER 1

Introduction

Climate Change in the Western Antarctic Peninsula: physical & biological interactions

The Western Antarctic Peninsula (WAP) is experiencing one of the most rapid rates of warming on Earth; since 1950 the annual mean midwinter air temperature has increased by 6°C (Vaughan et al. 2003). The WAP is also a region of high seasonal productivity due to upwelling of warm, nutrient rich Upper Circumpolar Deep Water onto the continental shelf, resulting in warming of the region with increased ocean heat content (Martinson et al. 2008, Ducklow et al. 2012). Decadal-scale climate oscillations due to the Southern Annular Mode (SAM) and El Niño Southern Oscillation (ENSO) also impact climate variability in the WAP (Stammerjohn et al. 2008b). As a result of long-term warming sea ice in the WAP advances later and retreats earlier, resulting in shorter ice seasons, and coverage that has decreased by 40% since 1990 (Stammerjohn et al. 2008a).

Sea ice dynamics are intrinsic to the ecosystems of the Southern Ocean. Changes in magnitude and timing of sea ice cover over the last few decades, especially in the northern WAP, have led to a latitudinal 'climate gradient'. These changes have affected the pelagic food web from plankton to top-predators (Stammerjohn et al. 2008a, Vernet et al. 2008, Montes-Hugo et al. 2009, Steinberg et al. 2012b, Garzio & Steinberg 2013). In the far northern WAP, these changes include an 89% decrease in chlorophyll *a* since 1979 (Montes-Hugo et al. 2009) and dramatic declines in ice-dependent Adelie penguins (*Pygoscelis adeliae)* (Ducklow et al. 2012). In contrast, in the southern WAP where sea ice persists, chlorophyll *a* has increased 66% during the same period and no decline in Adelie penguins is apparent.

Macrozooplankton abundance and composition in the WAP also reflect the changes occurring throughout the Antarctic marine ecosystem due to climate change (Ross et al. 2008, Steinberg et al. in review). Data from net tows in the Southern Ocean from 1926-2003 show a significant decrease in Antarctic krill (*Euphausia superba*) from 1976-1996 in the northern WAP region, while salp densities have increased throughout much of the entire Southern Ocean (Pakhomov et al. 2002, Atkinson et al. 2004). However, a recent analysis (Steinberg et al. in review) indicates no decrease in *E. superba* in the WAP from 1993-2013 and demonstrates a 5-year cycle in abundance peaks. Significant long-term changes in other taxa include an increase in the krill *Thysanoessa macrura*, and in some carnivorous taxa (polychaete *Tomopteris* sp., and amphipods) (Steinberg et al. in review). Zooplankton community structure directly affects carbon export through fecal pellet production, and changes in the zooplankton could potentially impact biogeochemical cycling in the WAP as well as affect trophodynamics (Ducklow et al. 2001, Turner 2002, Ducklow et al. 2008, Steinberg et al. 2012, Atkinson et al. 2012a, Gleiber et al. 2012). Whereas these studies document change in the dominant macrozooplankton in the WAP, whether long-term climate-mediated changes in the WAP are reflected in copepod abundance, distribution, or community structure remains unknown.

Importance of copepods in the Southern Ocean

Copepods dominate mesozooplankton in the Southern Ocean numerically, and often in biomass. Furthermore, copepods play a critical role in the pelagic food web as grazers of phytoplankton and microzooplankton, and as food for carnivores (Hopkins

1985, Conover & Huntley 1991, Atkinson 1998, Schnack-Schiel 2001). Southern Ocean copepods are adapted to the seasonally productive polar environment with variations in feeding strategy and life cycle ranging from some herbivorous species with winter diapause, feeding during summer months, to other species feeding year-round as omnivores and detritivores, and carnivorous species feeding primarily on smaller copepods (Marin 1988, Yen 1991, Atkinson 1998). Most species exploit the spring/summer bloom when the dominant copepod species can ingest up to 30% of their body carbon daily from phytoplankton and daily carbon ingestion can be up to 50% of primary production (Schnack-Schiel et al. 1985, Atkinson & Shreeve 1995, Li et al. 2001, Calbet et al. 2006). In comparison, recent studies during summer months in the WAP found a relatively low grazing impact of the dominant macrozooplankton (krill, pteropods, salps) that grazed on average <1% of primary production (excluding large salp blooms which grazed up to 169%) (Bernard et al., 2012). Instead microzooplankton are the dominant grazers in the WAP, consuming 32% to more than 100% of primary production (Garzio et al. 2013). However, the role of mid-size/trophic level zooplankton, the copepods in grazing of phytoplankton is still unknown in the WAP and is crucial to understanding food web dynamics and energy transfer (Sailley et al. 2013).

In addition to exerting grazing pressure, copepods are also important in export of particulate organic matter via production of dense, rapidly sinking, fecal pellets. A recent study examining the contribution zooplankton fecal pellets in WAP sediment trap samples found that copepods had the second highest contribution by taxa (after krill) to carbon flux from fecal pellets, contributing an annual average of 22% of the total fecal pellet POC flux (compared to 72% for krill fecal pellets) (Gleiber et al. 2012).

Furthermore, some species of copepods in the WAP are known to migrate vertically to below the mixed layer each day (Zmijewska & Yen 1993, Marrari et al. 2011b), and thus could facilitate export of POC by actively transporting POC consumed in surface waters via egestion of fecal pellets at depth (Schnetzer & Steinberg 2002, Steinberg et al. 2008). Thus, studies in the WAP on copepod contribution to flux, as well as grazing, would further elucidate their importance in biogeochemical cycling and carbon export, as well as help predict how climate–related changes in individual species might impact contribution of copepods to grazing and export.

Copepods and environmental change

Copepods, and other mesozooplankton, have relatively short life cycles which make their populations tightly coupled to environmental conditions, thus they are important indicators of the effects of climate change on pelagic ecosystems (Richardson 2008, Mackas & Beaugrand 2010). Zooplankton comprise important links in the food web between primary production and higher trophic levels and changes in the zooplankton populations can alter ecosystem structure (Steinberg et al. 2012a). Pelagic ecosystems in the Northern Hemisphere are already experiencing the effect of climate change on copepods resulting in the loss of commercially important upper trophic levels (Chiba et al. 2006, Mackas & Beaugrand 2010, Hunt et al. 2011). For example, in the north-east Atlantic there have been significant geographical shifts since the mid-1980's in the copepod community due to warming (Beaugrand et al. 2002), which may have resulted in decreased recruitment of Atlantic cod larvae due to mismatch in timing between the larval fish and peaks in copepods of suitable size for them to consume

(Beaugrand et al. 2003). Similar changes have been hypothesized for copepods in the Southern Ocean (Mackas & Beaugrand 2010, Constable et al. 2014), and could have detrimental effects on the pelagic food web.

Sea ice extent and duration in the Southern Ocean dictate the timing and magnitude of the spring/summer bloom that is crucial for food availability, reproductive timing and larval success of many copepod species (Atkinson et al. 2012b, Burghart et al. 1999, Tarling et al. 2004). Furthermore, polar zooplankton are sensitive to temperature; increases in temperature result in higher growth and metabolic rates, but higher metabolic demands can also result in a loss or range shift of some species (Ikeda et al. 2001, Mackey et al. 2012, Ward et al. 2014). Prior studies in the Southern Ocean have found short-term correlations between copepod abundance and environmental variables including temperature, chlorophyll *a,* sea ice cover, and salinity (Atkinson & Shreeve 1995, Burghart et al. 1999, Marrari et al. 2011a, Mackey et al. 2012). However, this is the first research to evaluate how copepods respond to environmental changes over the long term, and to explore the effects of sub-decadal climate oscillations on copepod populations. Long-term tends in the dominant macrozooplankton indicate correlations with environmental variables and climate indices that vary among taxa (Loeb et al. 1997, 2008; Loeb and Santora 2013; Ross et al. 2008, in press; Saba et al. 2014; Steinberg et al. in review). For example, Steinberg et al. (in review) recently found that trends in some of the dominant macrozooplankton (including chaetognaths, polychaetes, amphipods, salps and pteropods) were best explained by climate indices (Southern Annular Mode, and the El Niño/Southern Oscillation), due to higher abundances in lower ice conditions. Similar time-series analysis with copepods will further our understanding of changes in the WAP

region due to warming and suggest implications for the future of the pelagic marine ecosystem there.

Goal and structure of thesis

In my thesis I explore long-term changes in copepod species composition and abundance and evaluate the impact of copepods on biogeochemical cycling through grazing and fecal pellet production along the WAP. This study is the first examination of long-term trends in copepod abundance and the relationship between those trends and environmental variables/climate indices in the Southern Ocean. Furthermore, this is the most comprehensive picture to date of the role of copepods in grazing and carbon export in the southern WAP. The thesis is divided into four chapters, as follows:

Chapter 1– introduces the thesis.

Chapter 2– describes copepod community composition and abundance in the WAP over a 21-year time series (1993-2013) and examines long-term trends as related to environmental variables (chlorophyll-*a*, primary production, sea surface temperature, sea ice parameters) and climate indices (Southern Annular Mode, and the El Niño/Southern Oscillation). Variations in abundance and species composition along latitudinal and cross-shelf gradients are also evaluated.

Chapter 3– presents results from field experiments quantifying grazing impact and fecal pellet production of the large, dominant copepod species. I quantified copepod grazing rates using gut fluorescence analysis of individual animals to determine initial gut content and gut evacuation rate. I also examined egestion rates with elemental analysis of fecal pellets and animals. I determined the impact of copepod grazing on primary

production and phytoplankton standing stock, as well as daily body rations, and compared these between bloom and post-bloom conditions. I compare all my results with previously published studies that examined grazing, and egestion for meso- and macrozooplankton.

Chapter 4– concludes the thesis with a summary of my results, implications of my findings, and provides suggestions for future research.

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CHAPTER 2

Long-term change in the copepod community along the Western Antarctic Peninsula

ABSTRACT

Copepods are the dominant mesozooplankton taxa in the Southern Ocean, but long-term changes in their abundance and distribution along the Western Antarctic Peninsula (WAP), a region experiencing rapid climate warming, are unknown. We examined summer (January-February) copepod abundance along the WAP over two decades (1993-2013) and investigated long-term trends in copepod abundance with environmental parameters (sea ice, phytoplankton biomass and productivity, climate indices, and sea surface temperature). Copepods were numerically dominant, and comprised on average 81% of the total mesozooplankton abundance in the WAP. Seven taxa constituted 96% of WAP total copepod abundance (*Metridia gerlachei*, *Oithona* spp., *Calanoides acutus*, Clausocalanidae, *Paraeuchaeta antarctica, Oncaea* spp., and *Rhincalanus gigas*), and *Calanus propinquus* was an important contributor to copepod biomass. A significant long-term increase in total copepod abundance was found, with mostly positive anomalies from 2005-2013. Variation in abundance was best explained by sea ice retreat and chl *a* concentration, with higher abundances in lower ice and higher chl *a* conditions. Trends for individual species generally followed those of total copepods. Herbivorous copepods relying on the spring bloom were more abundant following an early sea ice retreat and during years of high summer chl *a*. In addition, *C. acutus* abundance was closely connected to the Southern Annular Mode (SAM), with higher abundance following positive SAM and lower ice conditions. The large, omnivorous copepod *C. propinquus*, and carnivorous copepod *P. antarctica* significantly

increased over time. Omnivorous copepods that spawn year-round had weaker relationships with sea ice, chl *a* concentrations, and primary productivity, but abundance anomalies still suggested an increase over time. Our results suggest mechanisms leading to interannual variability of summer copepod abundance in the WAP that can be used to predict how the plankton community will respond to future environmental changes.

1. INTRODUCTION

Copepods are the numerically dominant mesozooplankton in the Southern Ocean (Conover & Huntley 1991). They are highly adapted to the short growing season and low temperatures that characterize the polar environment with a range of feeding and life cycle strategies (Atkinson 1998). Copepods play a critical role throughout the Southern Ocean as grazers of phytoplankton and microzooplankton and as food for carnivorous zooplankton (Dubischar & Bathmann 1997, Kruse et al. 2010). Furthermore, they contribute to export of particulate organic matter via fecal pellet production (Gleiber et al. 2012). A number of prior studies of copepods in the Southern Ocean have focused on the abundance and distribution, as well as life cycle and feeding strategies, of the dominant species (Conover & Huntley 1991, Atkinson 1998, Schnack-Schiel 2001, Atkinson, Ward, et al. 2012). However, only a few studies have examined their abundance and distribution in the waters west of the Antarctic Peninsula (Ashjian et al. 2004, 2008; Lawson et al. 2004; Marrari et al. 2011), one of the most rapidly warming regions on Earth (Vaughan et al. 2003, Ducklow et al. 2012), and none has examined potential long-term changes in copepods due to warming or other environmental influences.

The Western Antarctic Peninsula (WAP) is a region characterized by high seasonal productivity that supports an ecosystem with large summer phytoplankton blooms and high summer abundance of krill that are food for upper trophic levels, such as seabirds and marine mammals (Ducklow et al. 2012). However, decreases in the magnitude and changes in the timing of seasonal sea ice cover in the WAP over the last

few decades, due to rapid warming, have led to a latitudinal 'climate gradient', affecting food web dynamics with changes at all trophic levels (Ducklow et al. 2012, Montes-Hugo et al. 2008, Stammerjohn et al. 2008a). For example, in the northern WAP there has been an 89% decrease in phytoplankton biomass (chlorophyll *a*) since 1979, while in the southern WAP where sea ice persists, there has been a 66% increase in phytoplankton biomass during the same period (Montes-Hugo et al. 2009).

Macrozooplankton abundance and community structure are also affected by changes occurring throughout the WAP (Ross et al. 2008; Steinberg et al. 2012b, in review). Data from net tows in the Southern Ocean from 1926-2003 show a significant decrease in Antarctic krill (*Euphausia superba*) from 1976- 1996 in the northern WAP region, while salp densities have increased (Atkinson et al. 2004). However, a recent analysis by Steinberg et al. (in review) indicates no long-term decrease in *E. superba* in the WAP from 1993-2013, rather a 5-year cycle in abundance peaks. Long-term changes in other taxa have been significant, including an increase in the krill *Thysanoessa macrura* and in some carnivorous taxa (polychaete *Tomopteris* sp., and amphipods) (Steinberg et al. in review). Abundances of macrozooplankton also correlate with sea ice, phytoplankton, and temperature, as well as decadal-scale climate oscillations such as the El Nino Southern Oscillation (ENSO) and Southern Annular Mode (SAM) (Loeb et al. 2008, Loeb and Santora 2012, Saba et al. 2014, Steinberg et al. in review). An inverse-model for the WAP food web further indicates a shift over the last decade in the northern WAP from an herbivorous system, with krill as the dominant grazers, to a microbial system where microzooplankton are the dominant grazers (Sailley et al. 2013).

While recent analyses document long-term change and effects of environmental variables on the dominant macrozooplankton in the WAP, spatial and temporal information on copepods in the region was inadequate to ascertain any long-term change. This is despite the fact that copepods are the most abundant mesozooplankton taxa year-round, and in summer they can have an impact on grazing of phytoplankton similar to krill in some regions (Bernard et al. 2012, Chapter 3). Copepods have short life cycles, relative to other zooplankton, that span multiple generations per year (small copepods) to 2-years (large copepods) at higher latitudes (Atkinson et al. 1997, Schnack-Schiel 2001, Chiba et al. 2002). Thus, they are important indicators of the effects of climate change on pelagic ecosystems (Richardson 2008, Mackas & Beaugrand 2010).

A few studies in the WAP provide a snapshot of the copepod community in the fall and winter of 2001 and 2002 in Marguerite Bay (Ashjian et al. 2004, Marrari et al. 2011b), but most previous studies of copepods in the WAP took place near the northern tip (Atkinson & Sinclair 2000; Mackey et al. 2012; Ward et al. 2012a, 2014). In addition, we lack long-term information on potential environmental drivers of changes in copepod abundance. Prior studies examined correlations with phytoplankton, temperature, salinity, and sea ice cover spanning one or two years (Atkinson & Shreeve 1995, Burghart et al. 1999, Ward et al. 2004, Marrari et al. 2011b). Hypothesized changes in the copepod community in the Southern Ocean include a poleward range shift of sub-Antarctic species, decreases in polar species, and changes in phenology due to warming (Mackas & Beaugrand 2010, Mackey et al. 2012, Ward et al. 2014, Constable et al. 2014), as has been seen in the Northern Hemisphere (Beaugrand et al. 2002, Chiba et al. 2006, Richardson 2008, Hunt et al. 2011).

In this study we examine long-term changes in copepod abundance in the WAP, and what environmental parameters may be driving these changes. We examined total copepod and individual species/taxa abundance and distribution in summer over two decades (1993-2013) across the broad continental shelf along the WAP, as part of the Palmer Antarctica Long-Term Ecological Research (PAL LTER) program. We further investigated how environmental parameters (sea ice, phytoplankton biomass and productivity, climate indices, and sea surface temperature) may be driving long-term trends in copepod abundance. Our results suggest mechanisms leading to interannual variability of summer copepod abundance in the WAP that can be used to predict how the copepod community will respond to future environmental changes.

2. MATERIALS AND METHODS

2.1 Study area and cruises

The Palmer Antarctica Long-Term Ecological Research (PAL LTER) grid, located along the western Antarctic Peninsula, consists of sampling transect lines spaced 100 km apart extending from Palmer Station in the north (64.77°S, 64.05°W) to Charcot Island in the south (69.45°S, 75.15°W) (Figure 2.1). Along each line, stations are spaced 20 km apart from the coast to 200 km offshore (Waters & Smith 1992, Ducklow et al. 2012). Zooplankton have been collected on annual research cruises in the austral summer (approximately 01 January – 10 February) since 1993. Sampling was conducted onboard the *MV Polar Duke* from 1993-1997 and the *ARSV Laurence M. Gould* from 1998-present (Ross et al. 2008, Steinberg et al. in review).

2.2 Zooplankton collection and analysis

Copepods and other mesozooplankton were collected from 0-300 m in double oblique net tows using a 1x1m rectangular frame net with 333 µm mesh and cod end. These tows are one of two types routinely performed on PAL LTER cruises (a larger, 2x2m frame, 700 µm mesh net is used to target larger macrozooplankton such as krill, salps, and pteropods; patterns in their abundance can be found in Ross et al. 2008, in press; Bernard et al. 2012; Steinberg et al. in review). The volume of water filtered was measured with a General Oceanics flowmeter attached to the net frame. Net depth was determined by a Temperature-Depth Recorder attached to the bottom of a conducting

hydrowire. From 1993-2008 tows were conducted at each PAL LTER grid station from the 600 to 200 lines, and from 2009-present on a modified grid extended to the -100 line in order to include a region with longer duration and greater extent of sea ice (Steinberg et al. in review). Tow duration was about 45 minutes at a ship speed of 2.0-2.5 knots. Once onboard usually all *Euphausia superba* and salps (mostly *Salpa thompsoni*) were removed from the sample, enumerated, measured for body length and biovolume (ml), and preserved separately. The biovolume of the remainder of the sample (minus *E. superba* and salps) was measured, and preserved in 4% buffered formaldehyde and stored for subsequent laboratory analysis. Abundance of juvenile and adult *E. superba* or salps (mostly *S. thompsoni*) are not included in this analysis (Steinberg et al. in review). Copepod nauplii were present in some tows, but were not enumerated, as the net mesh size was too large to sample them quantitatively.

We analyzed samples from subregions representative of the north-south, and coastal-slope gradients of the WAP, including one coastal, one shelf, and one slope (cross-shelf) station on each of the 600, 400, 200, and -100 sampling lines (Figure 2.1) in each year of the 21-year time series (1993-2013). Our analyses consider the entire PAL LTER grid area ('full grid'), as well as each latitudinal sub-region (600 = 'far north', 400 = 'north', 200 = 'south', -100 = 'far south') and cross-shelf region ('coast', 'shelf', 'slope'). Latitudinal sub-regions are based on hydrographic and sea ice conditions (Martinson et al. 2008, Stammerjohn et al. 2008a) and changes in penguin diet (W. Fraser pers. comm.), and cross-shelf gradient is described in Martinson et al. (2008). To reduce any variation due to zooplankton diel vertical migration, most samples analyzed were

from daytime tows (hours of darkness are limited to <4 hr. during our sampling period in January).

Preserved samples were sieved into three size fractions (>5 mm, 1-5 mm, and 0.33-1 mm) For the latter, a 0.2 mm screen was used as the smallest sieve to ensure no animals were lost (but we consider the collection net mesh size as the minimum size cut-off). The entire >5mm size fraction was enumerated, and the two smaller size fractions were subsampled as follows: the 1-5mm size fraction was split with a Folsom Plankton Splitter (1-1/64 sample enumerated), and the 0.33-1 mm size fractions were subsampled using a Stempel pipet (1-1/180 sample enumerated; Postel et al., 2000). The samples were analyzed using an Olympus SZX10 dissecting microscope with dark/bright field illumination at 8-20x magnification. Copepods were identified to species, genus or family, depending on presence of adult stages to confirm identification (Bradford-Grieve et al. 1999, Vervoort 1951); all other zooplankton were identified by major taxon (see Appendix 1 for details of zooplankton groups enumerated). The total abundance for each species or taxon (ind. 1000 m^{-3}) was calculated by multiplying by the appropriate split for each size fraction, summing the three size fractions, and dividing the abundance per sample by the volume of water filtered through the net (Alden et al. 1982).

2.3 Biovolume analysis and biomass calculation

To estimate copepod biomass, samples from the three most recent years (2011-2013) were analyzed using an optical imaging system to identify and measure copepod species. Size-fractionated zooplankton samples (or sub-samples, if animals were too numerous) were scanned and digitized using the ZooScan optical imaging system at a

resolution of 2400 dpi (Gorsky et al. 2010). ZooScan images were processed using ZooProcess and PkID software to detect, enumerate, measure, and classify the digitized images (Gorsky et al. 2010). Individual biovolume (mm^3) for each copepod species was calculated using measurements of copepod prosome length and width from digitized silhouette images, and applying an ellipsoid volume formula. We used the mean (± SD) dry weight (mg) of larger, abundant copepods (C*alanoides acutus* = 0.83 ± 0.40, adult *Paraeuchaeta antarctica* = 4.41 ± 1.45, *Calanus propinquus* = 1.53 ± 0.32, *Rhincalanus gigas* = 1.27 ± 0.36) described in Chapter 3 to calculate a body volume to dry weight conversion. We applied this volume:dry weight conversion to the mean biovolume (mm^3; measured from Zooscan) of all other species to calculate dry weight (mg) per individual copepod. We calculated the total community biomass for each species or taxon (mg dry wt. 1000 m^{-3}) by multiplying the individual dry weight (mg) by the abundance (ind. 1000 m^{-3}).

2.4 Data analysis

Annual abundances were calculated for the whole PAL LTER grid area from the mean abundance in all tows. Sub-region mean abundances were calculated separately for latitudinal (far north, north, south, far south) and cross-shelf (coast, shelf, slope) sub-regions. Rank Sum and ANOVAs run in SigmaPlot 11.0 were used to compare copepod abundance and percent composition by species between different latitudinal and cross-shelf sub-regions.

2.5 Annual abundance anomaly calculation

Annual anomalies for copepod species, and other zooplankton taxa were calculated for the whole PAL LTER grid area, and separately for latitudinal and cross-shelf sub-regions as in Steinberg et al. (in review). Abundance (or biomass) anomaly (A') was calculated using the formula:

$$A'_y = \log_{10}[\bar{A}_y / \bar{A}]$$

where $\bar{A}_y$ is the mean abundance (or biomass) for year y, and $\bar{A}$ is the mean of the yearly means (O'Brien et al. 2008). The direction of the anomaly (i.e., positive or negative) can be compared between copepod species and sub-region, but the relative magnitude of the annual anomaly should only be compared with others of the same species within the same sub-region since each was calculated separately (Steinberg et al. in review).

2.6 Environmental variables and climate indices

To examine environmental effects on copepod abundance we considered the following environmental variables in our analyses: phytoplankton chlorophyll *a* (chl *a*) and primary production (PP), sea-surface temperature (SST), and sea ice parameters (duration, ice days, day of advance and day of retreat). Methods for measuring chl *a*, PP, SST, and sea ice parameters are described in Steinberg et al. (in review) and Stammerjohn et al. (2008a). All environmental variable data are available at: http://oceaninformatics.ucsd.edu/datazoo/data/pallter/datasets. Annual anomalies for chl *a*, PP, SST, and sea ice parameters were calculated in the same manner as copepod abundance anomalies. We also examined the effect of sub-decadal climate oscillations known to influence the Western Antarctic Peninsula: the Southern Annular Mode (SAM) (http://www.nerc-bas.ac.uk/icd/gjma/sam.html), and the Multivariate El Niño Southern

Oscillation index (MEI) (http://www.esrl.noaa.gov/psd/people/klaus.wolter/MEI/) (Stammerjohn et al. 2008b, Loeb et al. 2008, Loeb & Santora 2013, Saba et al. 2014). We use both annual indices and seasonal components: spring (Sept. – Nov.), summer (Dec. – Feb.), autumn (March – May), and winter (June – Aug.).

2.7 Comparison with environmental parameters and climate indices

Stepwise multiple linear regressions, with data as annual anomalies, were performed to determine the most important environmental variables and climate indices accounting for variability in total copepod abundance, and that of individual copepod species. Parameters included in the model were: chl *a*, PP, SST, the four ice variables, and two climate indices (both annual and seasonal components). To investigate influential parameters resulting from this analysis further, we also performed individual regressions between time series (in annual anomaly form) of these environmental parameters and climate indices and copepod abundance.

Regional differences, and time lags between the various environmental parameters and copepod abundance, were considered in our analyses. For sea ice latitudinal sub-region analyses, we used annual anomalies for sea ice parameters measured along the peninsula (i.e. Anvers Island in the far north/north, Avian Island in the south). Although included in full grid analyses, we did not include the far south (-100 line) in our regional regression analyses, as there were only five years of data from that region. Regression analyses include environmental variables and climate indices concurrent with the time of summer (Jan/Feb) sampling (0 lag; for chl *a*, PP, and SST only) and with a 1-2 year lag (i.e., prior 1-2 calendar years or Jan/Feb periods, as

appropriate; for chl *a*, PP, sea ice parameters and climate indices). For example, a significant relationship between copepod abundance and 1-yr. lag in ice retreat would indicate that the Julian day of ice retreat in the austral spring affected copepod abundance the following January. 0-1 yr. lag is considered for total copepods, and individual species. 2-yr lag is only considered, as appropriate, for *C. propinquus*, *C. acutus*, *P. antarctica* and *R. gigas,* species known to have a 1-2-yr. life cycle at higher latitudes in the Southern Ocean (Atkinson 1991, 1998; Atkinson et al. 1997; Schnack-Schiel 2001; Chiba et al. 2002).

The stepwise multiple regression models included variables that explained more than 10% of variation. Model diagnostics were performed to avoid co-linearity and influential outliers. All regression analyses and diagnostics were performed using SAS statistical software. Significance for all statistical analyses was a priori at $\alpha = 0.05$.

2.8 Principal component analysis

We used principal component analysis (PCA) to analyze the spatial and temporal similarity among copepod species, as well as effects of environmental variables and climate indices. PCA included the most abundant copepods (annual abundance anomaly), environmental variables (in anomaly form), and climate indices, determined from regression analyses (above). PCA was performed in JMP 11.0.0 for the full grid area, as well as each sub-region. To examine long-term variations in groupings of copepod species, we also performed separate PCA for the first (1993-2003) and second (2004-2013) halves of the time series.

3. RESULTS

3.1 Copepod abundance and composition

3.1.1 Full grid

Copepods are the numerically dominant mesozooplankton taxa throughout the WAP and present in all tows enumerated (n = 201), with a mean (±SD) abundance of 7.0 (± 9.2) ind. m^{-3} (range = <0.1 – 67.5 ind. m^{-3}) (Table 2.1). Copepods comprised, on average, 81% of total mesozooplankton (range = 24 – 99%). After copepods, the most abundant mesozooplankton taxa were chaetognaths (6%), larval euphausiids (5%), ostracods (4%), and polychaetes (2%). (See Appendix 1 for higher taxonomic resolution abundance data. Note: *E. superba* juveniles, adults, and salps were not included in counts, see *Section 2.2;* copepod nauplii were not enumerated as the net mesh size was too large to quantitatively sample them). We excluded one tow (collected in 2011 in the far south and coast of the PAL LTER grid) from the mean abundance calculations for all taxa, since total copepod abundance (179 ind. m^{-3}, mostly *Calanoides acutus* and *Metridia gerlachei*) was 2.5 times greater than the second largest total copepod catch for the entire time series. This tow was included in the anomaly calculation.

The numerically dominant copepods throughout the WAP were *M. gerlachei*, *Oithona* spp., *C. acutus,* those in the family Clausocalanidae, *Paraeuchaeta antarctica* (mostly stage IV and V copepodites), *Oncaea* spp. and *Rhincalanus gigas* (Table 2.2, Figure 2.2a,b). Together these species comprised 96% of the total copepod abundance

(Table 2.2). The rarer copepods (mean = <100 ind. 1000 m^{-3}), included *Farrania frigida*, *Heterorhabdus* spp., *Scolecithricella minor*, *Calanus propinquus*, *Haloptilus* spp., *Gaetanus tenuispinus*, those in family Aetideidae, *Candacia* sp., *Euchirella* sp., and *Pleuromamma robusta* (Table 2.2, Figure 2.2c,d). Collectively the rarer copepods contributed to only 5% on average of the total copepod abundance, with a maximum of 30%. *Oithona* spp., Clausocalanidae, *Oncaea* spp., and *Scolecithricella minor* are smaller species (usually <1 mm in prosome length). *M. gerlachei, C. acutus* and *P. antarctica* copepodites were present in both <1 mm and 1-5 mm size fractions, and all other species were usually >1 mm (Table 2.3). *C. acutus* in the <1 mm size fraction were usually small copepodites. With the exception of *C. propinquus* (for which there was a high biomass), the rare copepods are not presented in our analyses.

3.1.2 Regional

Difference in total copepod abundance between latitudinal sub-regions was significant (1-way ANOVA, $p < 0.001$), with higher abundance (mean ± SD) in the far south (12.9 ± 11.6 ind. m^{-3}) than north (4.5 ± 5.1 ind. m^{-3}; Rank Sum, p = <0.001) and far north (6.5 ± 9.5 ind.m^{-3}; Rank Sum, p = <0.001), and greater abundance in the south (8.4 ± 10.5 ind. m^{-3}) than north (Rank Sum, p = 0.002) (Figure 2.2). Mean total copepod abundance increased from the coast (5.6 ± 5.3 ind. m^{-3}) to shelf (6.2 ± 9.6 ind. m^{-3}) to slope (9.6 ± 11.7 ind. m^{-3}), although this difference was not statistically significant (Figure 2.2).

Copepods were the most abundant mesozooplankton taxa in all sub-regions, increasing from far north (76 ± 14% of total) to far south (84 ± 9%), although this

difference was not significant. Copepod contribution to total mesozooplankton abundance slightly decreased from the coast (81 ± 13%) to shelf (78 ± 11%) to slope (76 ± 13%), with a significant difference between the coast and slope (Rank Sum, $p = 0.017$).

While the same copepod species generally dominated in each sub-region, the percent contribution differs among regions for some species. For example, *M. gerlachei* dominated the copepod community on the coast (42%) and shelf (34%), while on the slope they only contributed to 15% of total copepod abundance (1-way ANOVA, $p = <0.001$). *C. acutus* and *Oithona* spp. are the dominant copepod species on the slope, contributing to 30 and 26% of copepod species composition, respectively. Species composition also differed among latitudinal sub-regions. *R. gigas* comprised a lower proportion of total copepod abundance in the far south (0.5%) than in all other regions (1.7 – 2.3%; 1-way ANOVA, $p = <0.001$), and *C. propinquus* comprised a higher proportion in the far south (1.4%) than in the south (0.4%) and the far north (0.2%; 1-way ANOVA, $p = <0.001$).

3.2 Copepod biomass and composition

Individual copepod biovolume generally follows the same pattern as prosome length (Table 2.3). We used average measured dry weight (Chapter 3) to convert biovolume (Table 2.3) to dry weight, resulting in the following for each species (mg dwt mm^{-3}): *C. acutus* (0.17), *C. propinquus* (0.15), *P. antarctica* (0.12), *R. gigas* (0.08). We applied the average conversion of the first three (0.15 mg dwt mm^{-3}) to the measured biovolume of all other copepod species (except *Haloptilus* spp.) to calculate individual dry weight (mg dwt; Table 2.3). For *Haloptilus* spp., we applied the biovolume to dry

weight conversion for *R. gigas* of 0.08 mg mm^{-3} since both are transparent copepods, and lighter in weight relative to size than other species.

C. acutus and *M. gerlachei* dominated total copepod biomass, comprising 41 and 33% of total copepod dry weight, respectively. *P. antarctica, R. gigas* and *C. propinquus* are also important contributors to total copepod biomass (Table 2.2), as they are large-bodied copepods (Table 2.3).

3.3 Long-term trends in abundance and biomass

Total copepod abundance increased over the 21-year time series over the full grid area ($p = 0.031$, $r^2 = 0.221$), with a shift from mostly negative to positive anomalies post-2005 (Figure 2.3). Large, positive anomalies occurred every other year post-2005 (i.e. 2007, 2009 and 2011). Regionally, this increasing trend was stronger in the far north, and decreased (fewer positive anomalies) with increasing latitude (Figure 2.3). All cross-shelf sub-regions also exhibited this shift to mostly positive anomalies post-2005, with a significant increase in total copepods over the entire time series on the coast ($p = 0.017$, $r^2 = 0.27$) and shelf ($p = 0.040$, $r^2 = 0.20$). Total copepod biomass anomalies generally mirrored this trend (Figure 2.4), thus all further analyses are presented using abundance (ind. m^{-3}) data only

Although most copepod species generally mirror the long-term trends for total copepods across the full grid area and regionally, indicating a long-term increase, only *C. propinquus* and *P. antarctica* significantly increased over the time series (Figure 2.5). Both species had a strong shift from negative to positive anomalies post-2005 and significantly increased over the full grid, as well as most sub-regions, especially in the far

north (Figure 2.5). *R. gigas* alternated between positive and negative anomalies that persisted for 5-7 years over the time series: positive from 1994-1997, negative from 1998-2005, and positive from 2006-2012 (Figure 2.6a). This trend is regionally strongest in the far north and the north (Figure 2.6b). *C. acutus* follows the general long-term trends for total copepods, but large, positive anomalies also occurred throughout the time series (Figure 2.6c). Despite this, there is an indication of a long-term increase in *C. acutus* in the far north, with positive anomalies only occurring in the latter half of the time series (Figure 2.6d). *M. gerlachei*, *Oithona* spp., Clausocalanidae, and *Oncaea* spp., follow a similar trend (Appendix 2).

3.4 Trends with environmental variables and climate indices

Sea ice variables (1-yr. lag; i.e., year prior) and chl *a* (0-yr. lag) explained the greatest proportion of the variation in total copepod abundance in our stepwise multiple regression analyses (partial $r^2 = 0.45$ and 0.23, respectively; Table 2.4). This relationship was negative with sea ice and positive with chl *a* ($p < 0.05$). Higher abundance of copepods generally followed a year of low sea ice with early retreat, and vice versa (Figure 2.7). The highest copepod abundances of the time series occurred in the second of two consecutive years with high chl *a*, that itself also followed a year of low sea ice/early retreat (i.e., 2011). But, low chl *a* was not necessarily indicative of low copepod abundance. Regionally, sea ice had the greatest influence on copepod abundance, with the strongest negative correlation in the south ($p = 0.001$, $r^2 = 0.47$), and significant negative correlations in all sub-regions except the far north (Figure 2.8a,b; Appendix 3). Since total copepod abundance includes all species, these trends generally reflect those of

the most abundant species. For example, variation in abundance of Clausocalanidae is also best explained by sea ice variables (1-yr. lag) and chl *a* (0-yr. lag) (partial $r^2 = 0.41$ and 0.12, respectively; Table 2.4), with the strongest regional trend in the south ($p = <0.001$, $r^2 = 0.57$; Appendix 3) and significant correlations with sea ice in all sub-regions except the far north (Figure 2.7c,d). *M. gerlachei* and *Oithona* spp. show similar trends (Table 2.4), although these are weaker or non-significant in sub-regions (data not shown).

Sea ice (1-yr. lag) also accounted for most of the variation in *C. acutus* abundance, but SAM (Winter, 1-yr. lag) and chl *a* (0-yr. lag) were also important explanatory variables (partial $r^2 = 0.41$, 0.20, and 0.12, respectively; Table 2.4). Similar to the trends for total copepods, *C. acutus* abundance was higher following a year of low sea ice/early retreat, but also positively correlated with SAM resulting in peak abundances following years of positive SAM (Figure 2.9). These trends with sea ice and SAM were significant regardless of region; *C. acutus* had the strongest relationship with sea ice retreat in the far north ($p = 0.007$, $r^2 = 0.33$) and with SAM in the south ($p = <0.001$, $r^2 = 0.54$) and on the coast ($p = 0.001$, $r^2 = 0.43$; Figure 2.10, Appendix 3). Correlations were significant in the full grid area for *C. acutus* between smaller (<1 mm) animals, copepodite stages, sea ice (1-yr. lag; $p = 0.013$, $r^2 = 0.28$), and chl *a* (0-yr. lag; $p = 0.006$, $r^2 = 0.30$), but not significant for larger (>1.0 mm) animals.

For the large, omnivorous copepod *C. propinquus* and carnivorous copepod *P. antarctica,* primary production or chl *a* for the prior year explained the greatest amount of variation, followed by sea ice (1-yr. lag and 2-yr. lag, respectively; Table 2.4). This relationship is positive with primary production/chl *a,* and negative with sea ice. Regionally, *C. propinquus* was significantly positively correlated with primary

production in all regions except the far north and slope (Figure 2.11). On the slope there was a strong negative relationship between copepods and sea ice variables for the prior year ($p = <0.001$, $r^2 = 0.49$; Appendix 3). *P. antarctica* was significantly correlated with chl *a* only on the coast ($p = 0.022$, $r^2 = 0.26$). Primary production also accounted for the greatest proportion of variation for *Oncaea* spp. and *R. gigas* for the full grid area (0-yr. lag and 1-yr. lag, respectively; Table 2.4). This trend was significant and positive, but weak for both taxa. Regionally, *Oncaea* spp. abundance was not correlated with primary production, but *R. gigas* was positively correlated with primary production (0-yr. lag) on the slope ($p = 0.001$, $r^2 = 0.47$).

3.5 Principal Component Analysis (PCA)

In the Principal Component Analysis (PCA) for the full grid area, *C. acutus*, *Oithona* spp., and Clausocalanidae were an "anti-ice group", grouping closely together and in the opposite quadrat as sea ice parameters (1-yr. lag), indicating a negative response to higher sea ice conditions (Figure 2.12a). *Oncaea* spp., *P. antarctica*, and *R. gigas* ("PP group") group loosely and in the same direction as phytoplankton chl *a* and PP (and opposite *C. acutus*, *Oithona* spp., Clausocalanidae on component 1), indicating a positive response to higher phytoplankton biomass and production. *M gerlachei* and *C. propinquus* group closely together between the "anti-ice group" and "PP group", but did not have a high loading in component 1. Component 1 and 2 explained 59.1% of the variability (Figure 2.12a).

In exploring these relationships further, we found that copepod species grouped tighter in the far north compared to the south (Figure 2.12b,c). The north appears to be a

transition between the two, with some close groupings (data not shown). In the far north, Clausocalanidae, *Oithona* spp., *P. antarctica*, and *M. gerlachei* group tightly, indicating their abundances changed together over the time series (Figure 2.12b), but the loading is too weak in component 1 to draw further conclusions. *C. acutus* was in the opposite quadrat as sea ice variables (negative correlation) and same quadrat as SAM (positive correlation). *R. gigas* does not group with any other copepod species, but has the strongest loading on component 1 and is positively correlated with PP. In contrast, in the south species are spread out on both components, indicating less inter-annual cohesion in individual species abundance (Figure 2.11c). *C. acutus* and Clausocalanidae negatively correlated with sea ice, but the loading is weak in component 1. Component 1 and 2 explained 61.7% of the variability in the far north (Figure 2.12b) 53.2% of variability in the south (Figure 2.12c).

Comparing PCA for the earlier (1993-2003) and latter (2004-2013) half of the time series for the full grid area, we saw tighter grouping from 2004-2013, indicating species abundance changed together (with the exception of *R. gigas*). In comparison, species responded more variably in the earlier half of the time series, and were spread out in component 1 and 2 (Figure 2.13). Component 1 and 2 explained 52.9% of the variability from 1993-2003 (Figure 2.13a) 63.3% of variability from 2004-2013 (Figure 2.13b).

4. DISCUSSION

4.1 Composition and abundance of copepods in the WAP

Our results confirm that copepods are the numerically dominant mesozooplankton in the Antarctic Peninsula region (Zmijewska & Yen 1993; Voronina 1998; Cabal & Alvarez-Marqués 2002; Ashjian et al. 2004; Ward et al. 2005, 2014; Marrari et al. 2011). The majority of the copepod community (96% on average) was comprised of only a few taxa: *Metridia gerlachei, Oithona* spp., *Calanoides acutus*, family Clausocalanidae, *Paraeuchaeta antarctica* and *Rhincalanus gigas*. Prior studies also indicate these species generally dominate the copepod community in both abundance and biomass in the Antarctic Peninsula, as well as regions south of the Antarctic Polar Front (APF) (Hopkins 1985, Huntley & Escritor 1991, Ward et al. 2004, Marrari et al. 2011).

Abundances of total copepod and most species were lower (up to 2 orders of magnitude) in the WAP compared to the far northern tip of the Antarctic Peninsula near South Georgia, where most prior summer sampling has occurred (Table 2.5). Mesozooplankton generally decrease in abundance, diversity, and biomass with increasing latitude in the Southern Ocean (Foxton 1956, Voronina 1998, Atkinson 1998, Atkinson, Ward, et al. 2012, Ward et al. 2014). This is attributed to the biogeographic range overlap near the Antarctic Polar Front (APF), of warmer-water 'sub-Antarctic species', and cold-water 'Antarctic species' (Froneman et al. 2000, Pakhomov et al. 2000). Additionally, increased water temperatures result in earlier recruitment and

quicker growth of copepodites (Chiba et al. 2001, Ward et al. 2004, Mackey et al. 2012, Ward et al. 2012b). Copepod abundances in our study were similar to ice-free higher latitudes sampled in the summer months (Table 2.5).

There is only one prior study of individual copepod species abundances (Marrari et al. 2011) that overlaps our sampling region in the WAP (although Ashjian et al. 2004 reported copepod size classes). Marrari et al. (2011) sampled in the Marguerite Bay (Figure 2.1) in the autumn (April-May) of 2001 and 2002 found median total copepod abundances (46.3 and 28.3 ind. m^{-3} in 2001 and 2002, respectively) that were an order of magnitude higher than median abundances in our study, using the same mesh size (333μm) net. Individual species abundances reported in Marrari et al. (2011) were also an order of magnitude higher, with *C. acutus* abundance up to 30 times higher, although the upper range of *C. acutus* abundances we found were similar (Table 2.5). We expected to find higher copepod abundance in the summer months, following copepod recruitment, compared to fall during high larval mortality (Atkinson 1991). There are several explanations for the marked differences in abundance between the two studies. The most likely explanation for the discrepancy between the studies is that our January sampling missed the newly hatched nauplii and smaller copepodite stages, which are large enough by fall to be included in net hauls (Atkinson 1998). In a study near Marguerite Bay in the fall and winter of 2001, Ashjian et al. (2004) reported ~49-63% of copepods >2.5mm were CV (copepodite 5) stage *C. acutus*, likely too small to be sampled by our nets, 3-7 months prior. In addition, Marrari et al. (2011) sampled to 800 m and our sampling was restricted to the upper 300 m, possibly missing deeper-living copepods. While the majority of the literature suggests most of the copepod abundance is in the upper 200 m

in summer (Atkinson, Ward, et al. 2012), a study in the northern WAP examining seasonal differences in copepod abundance with depth found *M. gerlachei*, *P. antarctica*, *R. gigas* and *C. propinquus* often had abundances below 300 m equal to or higher than in the upper 300 m (Zmijewska & Yen 1993).

4.2 Regional abundance and distribution of copepods in the WAP

We found that average abundance of total copepods on the slope was twice as high as on the coast. Large chaetognaths *Pseudosagitta* spp., and euphausiids *Euphausia superba* and *Euphausia crystallorophias*, are comparatively more abundant on the shelf and coast of the WAP than the slope (Atkinson et al. 2004, Bernard et al. 2012, Loeb et al. 1997, Steinberg et al. in review). *Pseudosagitta* spp. primarily feed on copepods (Froneman & Pakhomov 1998, Kruse et al. 2010), and krill are also known to feed on copepods and have competitive interactions with them (Atkinson et al. 1999, 2002). The highest abundances of the Antarctic krill, *E. superba* (Steinberg et al. in review) and that of copepods (this study) never co-occurred, with the highest krill abundance restricted to the coast (Steinberg et al. in review), and the highest abundance of copepods occurring more frequently on the slope. Thus, we may have found lower abundances of copepods on the coast because they are preyed upon by macrozooplankton.

Individual copepod species followed this cross-shelf trend in abundance with the exceptions of *M. gerlachei* and *P. antarctica,* which were more abundant on the coast. This is consistent with previous work indicating these species are more abundant in shallower, shelf and coastal regions (Ward & Wood 1988, Zmijewska & Yen 1993). Additionally, sea ice may still persist during summer in coastal regions, especially in

years of later sea ice retreat. In the Weddell Sea, higher abundances of copepods occurred in open water and decreased with increased ice cover, with the exception of *M. gerlachei* (Siegel et al. 1992, Burghart et al. 1999). Seasonal changes in copepod distribution may be reflected in the abundance observations as well. Ashjian et al. (2004) examined cross-shelf abundances of copepods in the Marguerite Bay area in fall and winter for large (>2.5mm) and small (<2.5mm) copepods. Opposite to our results, they found higher abundances of small copepods (including *M. gerlachei*) on the slope, and higher abundance of large copepods (including *C. acutus*, *P. antarctica*, and *R. gigas*) on the coast.

In our latitudinal comparison we found higher abundances of total copepods in the southern WAP. The greatest difference in abundance was for *C. propinquus*, with average abundance in the far south over an order of magnitude greater than the far north, consistent with latitudinal variation described previously for this large, cold-water copepod (Atkinson 1991, Schnack-Schiel 2001). We found the opposite latitudinal trend for *R. gigas*, which was the only species comprising a significantly lower proportion of copepod abundance in the far south then northern sub-regions. *R. gigas* is associated with the Antarctic Circumpolar Current (ACC) and is often the most abundant copepod near the APF, and likely at the southern end of its range in our study region (Atkinson & Shreeve 1995, Cabal & Alvarez-Marqués 2002, Ward et al. 2004, Mackey et al. 2012).

4.3 Link between copepods, sea ice, and phytoplankton

Copepod abundance significantly increased in the WAP over the time series, likely due to decreasing sea ice with an earlier retreat and increasing chl *a* as indicated by

our multiple regression model. Many Antarctic copepod life cycles are adapted to a short, productive growing season, with reproduction in the spring/summer timed to coincide with the seasonal phytoplankton bloom, although variation exists among species (see *Section 4.4*; Voronina et al. 1980, Atkinson et al. 2012). This results in abundances up to ten times higher in the summer months (compared to the rest of the year), and declining thereafter due to larval mortality (Atkinson 1991, Schnack-Schiel & Mizdalski 1994, Hunt & Hosie 2006). Timing of sea ice retreat and onset of the spring bloom can also impact copepod abundance (Burghart et al. 1999). Studies in the mostly ice-free Scotia Sea in January found higher abundance of the copepods *C. acutus*, *R. gigas* and *C. propinquus* at later developmental stages compared to the Weddell Sea, where seasonal sea ice persists up to 9 months (Marin 1987; Atkinson et al. 1997; Ward et al. 1997, 2004). Thus, there is a delay in the timing of recruitment of up to three months with latitudinal variation in sea ice retreat and timing of the subsequent spring bloom. We expect an earlier sea ice retreat, and consequently earlier phytoplankton bloom and longer ice-free growing season in the WAP (Arrigo & Thomas 2004), to be favorable to copepod growth. The trend between copepod abundance and sea ice retreat was much stronger in the southern part of the WAP, where interannual variations in sea ice are more extreme (compared to the far north) and can more than double the phytoplankton growing season depending on the date of retreat (Stammerjohn et al. unpublished data).

Primary production and chl *a* for both the current (0-yr. lag) and prior season (1-yr. lag) were strongly positively correlated with total copepod abundance, indicating the additive effect of two consecutive years of sustained higher phytoplankton production on copepod abundance, and thus recruitment success. Some larger copepod species (e.g., *C.*

acutus, *R. gigas* and *C. propinquus*) can take two years to reach adulthood, especially in regions with short summer growing seasons (Atkinson et al. 1997, Ward et al. 1997, Atkinson 1998, Schnack-Schiel 2001). Thus, with two years of high PP the population would benefit from high food availability for both early and later stage copepodites to survive overwinter (or two winters) and reproduce the following spring.

Since our study relies on annual summer sampling, the interannual variations in copepod abundances likely reflect both seasonal abundance peaks and the timing of recruitment (Mackas & Beaugrand 2010). For example, earlier sea ice retreat allows more time between recruitment and our January sampling, thus we see higher abundances of copepods as larvae have more time to grow to a larger copepodite stage (Burghart et al. 1999). In contrast, later sea ice retreat would result in later recruitment, possibly coinciding with January sampling, and copepodites would be too small to be retained in our nets. Thus, the long-term increase in total copepods may reflect a shift to earlier recruitment, increase in summer abundance, or combination of the two. This change in phenology has also been suggested as an explanation for long-term increases in some macrozooplankton taxa in summer in this region of the WAP (Steinberg et al. in review).

4.4 Long-term trends for individual species

Sea ice retreat, as well as PP and chl *a,* were generally the best predictors of abundance of individual copepod species, with variations on this long-term trend reflecting differences in life cycle, feeding strategy, and generation time. Long-term increases in most copepod species (significant for *C. propinquus* and *P. antarctica*) likely are due to the decrease in sea ice, and increase in primary production and chl *a* in the

WAP, especially in the latter half of the time series (Stammerjohn et al. 2008a, Montes-Hugo et al. 2009, Ducklow et al. 2012). In fact, the long-term increase in copepod abundance we found for almost all species is driven by the shift from mostly negative to positive abundance anomalies in the latter half of the time series, especially in the far north.

Using PCA, we observed closer grouping of species in the 'far north' compared to 'south', indicating species abundance was changing together over the time series in the north as opposed to responding more variably in the south. This reflects the greater change in productivity and sea ice in the north WAP, resulting in similar success (high abundance) or failure (low abundance) for more species, while in the south this synergistic effect is not as evident. The PCA comparing the earlier and later halves of the time series indicates a similar trend, with a more synchronous copepod community in recent years which could further explain the similar shift from negative to positive anomalies for all species. However, we make this conclusion with caution, as the components 1 and 2 only account for 53-63% of the variation.

4.4.1 Herbivores with strong spring recruitment

Long-term variations in the abundance of *C. acutus* and those in the family Clausocalanidae were best explained by sea ice and chl *a*. As both species are predominantly herbivores having similar reproductive cycles with recruitment prior to the spring bloom and increase in abundance over 10-fold in summer months from the newly hatched cohort (Marin 1987, Fransz 1988, Atkinson 1991, Schnack-Schiel & Mizdalski 1994, Atkinson et al. 1997), our results are consistent with what is known about their life

history. In addition to significant negative trends with sea ice in all regions of the WAP, we found that positive anomalies in *C. acutus* also closely tracked positive SAM events (and vice versa). This trend was especially strong in the south and on the coast where sea ice persists longer. *C. acutus* is the only Antarctic copepod that undergoes true winter diapause, thus relying on the spring/summer bloom to build up their extensive lipid stores necessary for winter survival and reproduction the following spring (Hagen & Schnack-Schiel 1996, Atkinson 1998, Tarling et al. 2004). Since positive SAM events cause later sea ice advance and a shorter ice season with early retreat (Stammerjohn et al. 2008a, b), we posit that *C. acutus* copepodites benefit from the longer growing season, with higher overwinter success and recruitment the following spring. Indeed, prior studies show that *C. acutus* copepodites that are unable to reach later stages (~CIV or CV) by the end of the productive season are more susceptible to starvation (Bathmann et al. 1993). The strongest trends for *C. acutus* (positive correlation with SAM) and Clausocalanidae (negative with sea ice retreat) are in the southern part of the WAP, where decreases in sea ice over time can increase the growing season by over three months (S. Stammerjohn unpub). Considering that a newly hatched cohort of *C. acutus* can develop from CI to an overwintering CIV/CV stage in 1.5 months (Schnack-Schiel & Mizdalski 1994, Atkinson et al. 1997, Burghart et al. 1999), timing of sea ice can control reproductive success of their populations in the WAP.

Primary production (1-yr. lag) and chl *a* (0-yr. lag) best predicted the variation in the abundance of *R. gigas*, but this relationship was weak in most regions. Surprisingly there were no significant correlations between *R. gigas* and sea ice parameters, since *R. gigas* has a life cycle similar to *C. acutus* with spring/summer spawning and possible

winter diapause (Ward et al. 1997, Atkinson 1998). However, *R. gigas* has a more flexible life cycle that may help prevent crashes during years with shorter phytoplankton growing seasons, with generation times ranging from 1-2 years. Adult females are known to overwinter and spawn a second time at higher latitudes (Ward et al. 1997). This variable life cycle may explain sustained years of either high or low abundance anomalies in *R. gigas* over the long-term, but could also mask correlations with environmental variables.

4.4.2 Omnivores spawning year-round

Abundance of omnivorous copepods *M. gerlachei* and *Oithona* spp. increased in years with earlier sea ice retreat, and *Oncaea* spp. abundance increased with high primary production (0-yr. lag). These correlations with environmental variables were weaker compared to those we found for *C. acutus* and Clausocalanidae. This is not surprising as these species are omnivores and detritivores that remain active through the winter, thus they are less dependent on the spring bloom for recruitment and reproductive success (Metz & Schnack-Schiel 1995, Hagen & Schnack-Schiel 1996, Atkinson 1998, Kattner et al. 2003). Some studies have shown summer peaks in abundance (especially for *Oithona* spp.), but as these copepods have short life cycles with overlapping generations (Fransz 1988, Fransz & Gonzalez 1995, Metz 1996), it is difficult to interpret trends in their abundance with summer-only sampling.

4.4.3 Higher trophic level copepods

We saw a significant increase in the abundance of both the predatory copepod *P. antarctica* and the large, omnivorous copepod *C. propinquus* throughout the WAP. Our multiple regression models suggest both copepods have benefitted from increased primary production and chl *a*, and to a lesser extent decreased sea ice. Furthermore, their diet includes smaller copepods; thus the effects of increased primary production (and possibly decreased sea ice) are also manifested at higher trophic levels, since their small copepod prey may also increase under these conditions.

P. antarctica is almost entirely predatory, feeding on both large and small copepods, including *Metridia* spp., *C. acutus, Oncaea* spp., and *Oithona* spp. (Hopkins 1985, Oresland 1991). Studies of stage CV *P. antarctica* consumed, on average, 2-8 (and up to 20) prey items per day (Oresland 1991, Yen 1991). Considering that we found *P. antarctica* to contribute to an average of 10% of the WAP copepod population, they could have a significant top-down impact on the copepod community during summer. The majority of *P. antarctica* we found were copepodites (CIV or CV) and likely 6 months old, as prior studies have described reproduction peaks in July and January, with a 1-yr life cycle (Ward & Robins 1987, Oresland 1991, Alonzo et al. 2000). Thus, the long-term trends with chl *a* (1-yr. lag) and sea ice (2-yr. lag) correspond with their predatory feeding strategy and life cycle, as variations in the abundance of their prey (see above) also trend with chl *a* and sea ice.

Higher abundances of *C. propinqnuus* occurred one year after a year of high primary production, which is consistent with their life span, which is >1 year at higher latitudes (Atkinson 1998). Furthermore, a greater proportion of ripe females occur in years with high PP (Schnack-Schiel et al. 1991). *C. propinquus* reproduce during the

spring/summer bloom, but later than *C. acutus* since *C. propinquus* is less reliant on the spring bloom. *C. propinquus* is an omnivore, feeding on a range of carbon sources from diatoms to small copepods (i.e. *Oithona* spp. and *Oncaea* spp.) and remaining active through the winter (Hopkins 1987, Metz & Schnack-Schiel 1995). Compared to *P. antarctica*, *C. propinquus* was more strongly correlated with primary production the prior year, because *C. propinquus* feed on diatoms in addition to small copepods.

4.5 Long-term increase in the WAP copepods and comparison to predicted trends

We suggest that the observed increase in anomalies over the time series is the result of 1) a phenology shift with earlier recruitment, 2) higher abundance due to more "copepod-favorable" conditions, or 3) combined effect of both. Our hypotheses are similar to the changes seen in copepods in other parts of the world's oceans due to warming, as well as suggested changes in the Southern Ocean (Chiba et al. 2006, Constable et al. 2014, Hunt et al. 2011, Mackas and Beaugrand 2010, Mackey et al. 2012, Richardson 2008, Steinberg et al. in review). A shift in phenology is likely for the polar copepod *C. acutus*, with recruitment tied to the spring bloom. We saw significant relationships between chl *a* (positive) and sea ice (negative) with *C. acutus* copepodite abundance in the smaller size fraction (<1.0 mm). Therefore, higher abundance of smaller *C. acutus* results from these environmental conditions. These relationships were not significant for larger (>1.0 mm) *C. acutus.* This is consistent with prior studies in the northern WAP, and the Scotia and Weddell Seas, which report a spatial trend of younger copepod stages with increasing latitude, especially for *C. acutus* (Atkinson et al. 1997, Burghart et al. 1999, Ward et al. 2004, Ashjian et al. 2004). While temporal aliasing is

possible with once-per-year sampling, earlier recruitment for *C. acutus* leads to higher overwintering success as they can reach a larger copepodite stage before winter (Tarling et al. 2004), thus higher abundance the next season. Furthermore, the long-term increases in the abundance of copepods that reproduce in the winter (i.e. *P. antarctica*) or continuously with multiple generations throughout the year (i.e. *M. gerlachei, Oithona* spp., *Oncaea* spp.) (Oresland 1991, Fransz & Gonzalez 1995, Atkinson 1998) suggests an actual increase in abundance (as opposed to temporal aliasing).

We did not see evidence of a range shift for WAP copepods, such as increases in sub-Antarctic copepods or decreases in polar species, as observed in the North Atlantic (Beaugrand 2005, Chiba et al. 2006) and predicted for Southern Ocean copepods (Mackas & Beaugrand 2010, Mackey et al. 2012, Ward et al. 2014, Constable et al. 2014). The dominant copepods in the Southern Ocean are highly adapted to the interannual variability in the summer growing season, with flexible life cycles and feeding strategies (Atkinson 1998). In comparison, the polar regions of the northern hemisphere have more copepod species with a winter diapause that are more heavily reliant on the spring bloom (Conover & Huntley 1991). Furthermore, all the dominant copepod species we found in the WAP are known to occur in higher abundances at latitudes north of our study region with warmer water (Atkinson & Shreeve 1995; Ward et al. 2004, 2006). Thus, with current warming scenarios detection of an increase (decrease) in subpolar (polar) copepods at a given latitude may be more subtle in the Southern Ocean vs. the northern hemisphere.

5. CONCLUSIONS AND IMPLICATIONS WITH FURTURE CHANGE

We found lower copepod abundances in the WAP, compared to regions in the far northern Antarctic Peninsula, but increases in abundance over time indicate WAP copepods are positively responding to changes in the environment and climate. The environmental changes that best predicted years with higher copepod abundance were early sea ice retreat, higher primary production, and chl *a*. Thus, the long-term decrease in sea ice and its earlier seasonal retreat (Stammerjohn et al. 2008a), and increase in phytoplankton biomass and productivity observed in the WAP over the past 20-years (Montes-Hugo et al. 2009) have resulted in higher copepod abundances, likely with earlier copepod recruitment.

Further north of our study region chl *a* has decreased over time, due to increased winds which lead to reduced sea ice concentration early in the season (Montes-Hugo et al. 2009). As these increased winds move poleward with the expected southern shift of the latitudinal 'climate gradient' in the WAP, krill are predicted to be negatively impacted with sustained years of lower chl *a* (Saba et al. 2014). The herbivorous *Calanoides acutus* is known to rely heavily on the diatom spring bloom for extensive lipid build-up to survive overwinter during diapause (Tarling et al. 2004); thus, we may expect to see decreases in their abundance in the future. Furthermore, warming water temperatures would increase metabolic demands, and copepods could more quickly exhaust their lipid supply and be unable to survive the winter and reproduce. Studies in

the Bering Sea have shown seasonal decreases in similar polar copepods with winter diapause, due to warmer conditions (Coyle et al. 2011, Hunt et al. 2011).

While bottom-up control on the copepod community is evident, top-down control could become increasingly stronger due to the increase in predatory copepods and other zooplankton. We saw the most significant increases over the time series in the abundance of carnivorous copepods; furthermore, Steinberg et al. (in review) saw significant long-term increases in taxa known to prey on copepods (chaetognaths, polychaete worms, and amphipods). Thus, the higher abundances in copepods we saw due to more favorable growing conditions, may be limited in the future by higher predation. Recently, an inverse model approach for the WAP pelagic ecosystem indicated a change in carbon pathway from a diatom-krill-top predator food chain, to dominance by the microbial food web (Sailley et al. 2013). Sailley et al. (2013) also indicated that copepods can change the flow of carbon through the food web. Indeed, copepods in the WAP contribute to carbon cycling through flux of dense fecal pellets year round and grazing on primary production (Gleiber et al. 2012, Chapter 3). Thus, the long-term increase in copepod abundance, combined with changes in abundance of other zooplankton taxa in the WAP (Steinberg et al., in review), suggests that continued warming in the WAP may alter food-web dynamics and biogeochemical cycles.

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Table 2.1. Mean, standard deviation of the mean (SD), median, and maximum abundance (ind. 1000 m^{-3}) of major mesozooplankton taxa. Minimum abundance is 57 ind. 1000 m^{-3} for Copepoda, 3 ind. 1000 m^{-3} for Chaetognatha, and 0 ind. 1000 m^{-3} for all other taxa. n = 201 tows. % = proportion of mean abundance of each taxa. See Appendix 1 for abundances at higher taxonomic resolution. Mean abundances exclude one outlier tow with a total copepod abundance of 1.8 x10^5 ind. 1000 m^{-3}. *Euphausia superba* juveniles and adults, and salps are not included.

	Abundance (ind. 1000m^{-3})			
	Mean ± SD	**Median**	**Maximum**	**%**
Copepoda	7001 ± 9238	3990	67462	81.3
Chaetognatha	524 ± 618	302	4452	6.1
Euphausiacea - larvae	461 ± 1627	30	12455	5.3
Ostracoda	333 ± 458	159	2731	3.9
Polychaeta	154 ± 369	40	3506	1.8
Siphonophorae	57 ± 102	18	757	0.7
Pteropoda	36 ± 71	14	822	0.4
Amphipoda	35 ± 48	19	28	0.4
Cnidaria	11 ± 62	0	836	0.1
Teleostei	3 ± 11	0	97	<0.1
Decapoda	0.3 ± 2.1	0	28	<0.1
Cephalopoda - juvenile	<0.1 ± 0.1	0	1	<0.1

Table 2.2. Mean, standard deviation of the mean (SD), median, and maximum abundance (ind. 1000 m^{-3}) for copepods. Minimum abundance is <1 ind. 1000 m^{-3}. n = 201. Copepods identified as belonging to the family Clausocalanidae likely include *Clausocalanus laticeps* and *Ctenocalanus citer*, but adult males were absent, making identification difficult, and Clausocalanid-like copepodites comprised the majority of this taxa. Mean biomass (mg dry weight 1000 m^{-3}) calculated from mean abundance and measured or estimated individual dry weight (from Table 2.3). % = proportion of mean abundance or biomass of each species/taxa. Mean abundances exclude one outlier tow with a *Calanoides acutus* abundance of $1.5x10^5$ ind. 1000 m^{-3} and total copepod abundance of $1.8x10^5$ ind. 1000 m^{-3}.

	Abundance (ind. 1000m^{-3})				Biomass (mg dry wt. 1000m^{-3})	
	Mean ± SD	**Median**	**Max**	**%**	**Mean**	**%**
Metridia gerlachei	1996 ± 2434	1140	15966	28.9	849.3	32.5
Oithona spp.	1570 ± 4330	371	48615	22.7	17.2	0.7
Calanoides acutus	1402 ± 4186	352	42646	20.3	1156.7	44.3
Clausocalanidae	751 ± 1518	286	11165	10.9	24.1	0.9
Paraeuchaeta antarctica	664 ± 731	417	3965	9.6	293.1	11.2
Oncaea spp.	159 ± 324	34	2254	2.3	3.2	0.1
Rhincalanus gigas	122 ± 254	49	2423	1.8	154.7	5.9
Farrania frigida	72 ± 127	25	937	1.0	11.8	0.5
Heterorhabdus spp.	53 ± 95	18	844	0.8	27.6	1.1
Scolecithricella minor	51 ± 91	24	945	0.7	1.3	<0.1
Calanus propinquus	35 ± 87	10	791	0.5	53.4	2.0
Haloptilus spp.	23 ± 41	7	304	0.3	6.0	0.2
Gaetanus tenuispinus	11 ± 35	0	364	0.2	5.8	0.2
Aetideidae	5 ± 15	0	148	0.1	3.0	0.1
Candacia sp.	2 ± 17	0	234	<0.1	1.9	0.1
Euchirella sp.	1 ± 5	0	62	<0.1	4.1	0.2
Pleuromamma robusta	1 ± 2	0	17	<0.1	0.3	<0.1

Table 2.3. Summary of individual mean and standard deviation of the mean (SD) for biovolume and measured or calculated dry weight for each copepod species/taxa. Copepods are listed by decreasing dry weight. n = number of ZooScan vignettes for each species/taxa measured for prosome length and width. Copepod dry weight was measured for adult *Paraeuchaeta antarctica*, *Calanus propinquus, Rhincalanus gigas*, and *Calanoides acutus,* and calculated from the average biovolume:dry weight conversion for all other copepod species/taxa.

	Prosome length (mm)	**Copepod Biovolume (mm^3)**		**Copepod dry wt. (mg)**
	Mean ± SD	**Mean ± SD**	**n**	
Euchirella sp.	6.41 ± 0.44	30.26 ± 6.45	3	4.54
Paraeuchaeta antarctica - adult	7.40 ± 1.56	35.93 ± 18.15	130	4.41
Calanus propinquus	4.63 ± 0.78	10.46 ± 3.83	1195	1.53
Rhincalanus gigas	4.66 ± 1.70	16.66 ± 14.33	1329	1.27
Candacia sp.	3.78 ± 0.64	7.35 ± 1.79	17	1.10
Calanoides acutus	3.63 ± 0.64	4.90 ± 2.12	9245	0.82
Pleuromamma robusta	3.50 ± 0.02	4.13 ± 2.25	2	0.62
Aetideidae	3.74	3.74	1	0.56
Gaetanus tenuispinus	3.24 ± 0.49	3.64 ± 1.66	23	0.55
Heterorhabdus spp.	3.04 ± 0.69	3.45 ± 1.31	9	0.52
Metridia gerlachei	3.08 ± 0.42	2.84 ± 0.87	6251	0.43
P. antarctica - CIV, CV	2.48 ± 0.77	2.81 ± 2.28	1199	0.42
Haloptilus spp.	2.79 ± 0.64	3.47 ± 1.98	38	0.26
Farrania frigida	2.11 ± 0.47	1.09 ± 2.05	18	0.16
Clausocalanidae	1.18 ± 0.47	0.21 ± 0.19	115	0.03
Scolecithricella minor	0.97 ± 0.21	0.17 ± 0.08	23	0.03
Oncaea spp.	1.16 ± 0.15	0.13 ± 0.03	33	0.02
Oithona spp.	0.84 ± 0.12	0.07 ± 0.04	73	0.02

Table 2.4. Results of stepwise multiple regression analyses addressing the effect of environmental parameters and climate on copepod abundance. Stepwise multiple regression analyses from annual mean abundance anomaly for the full grid area for total copepods, and individual species (in order of abundance) are shown. Sea ice, primary production, and chl *a* variables are annual anomalies. Explanatory variables and statistical scores obtained from the best model among stepwise multiple regression analyses are shown. Test statistics include r^2 and p-values for the overall model, the coefficient (slope) for the regression equation, the standard error (SE) associated with the model coefficient, the 2 tailed p-value (*p*) used in testing the null hypothesis for each significant model variable, and the partial r^2. n = number of years included in the model.

Variable	n	Slope	SE	*p*	*Partial* r^2
Total Copepods (r^2 = 0.68, *p* = <0.001)	21				
Sea ice retreat (1-yr. lag)		-8.280	1.588	<0.001	0.451
Chl *a* (0-yr. lag)		0.830	0.236	0.002	0.228
Metridia gerlachei (r^2 = 0.41, *p* = 0.015)	19				
Sea ice retreat (1-yr. lag)		-5.332	2.141	0.024	0.220
Primary production (0-yr. lag)		0.378	0.169	0.040	0.186
Oithona sp. (r^2 = 0.51, *p* = 0.002)	21				
Sea ice retreat (1-yr. lag)		-10.424	2.766	0.002	0.361
Chl *a* (0-yr. lag)		0.945	0.405	0.031	0.148
Calanoides acutus (r^2 = 0.73, *p* = <0.001)	21				
Sea ice retreat (1-yr. lag)		-9.499	2.046	<0.001	0.406
SAM (winter, 1-yr. lag)		0.091	0.026	0.003	0.204
Chl *a* (0-yr. lag)		0.823	0.296	0.013	0.122
Clausocalanidae (r^2 = 0.54, *p* = 0.001)	21				
Sea ice retreat (1-yr. lag)		-9.076	2.210	0.001	0.412
Chl *a* (0-yr. lag)		0.706	0.324	0.043	0.123
Paraeuchaeta antarctica (r^2 = 0.59, *p* = 0.006)	20				
Chl *a* (1-yr. lag)		1.148	0.282	0.001	0.371
Sea ice retreat (2-yr. lag)		-5.767	1.945	0.009	0.215
Oncaea sp. (r^2 = 0.28, *p* = 0.020)	19				
Primary production (0-yr. lag)		0.627	0.245	0.020	0.278
Rhincalanus gigas (r^2 = 0.44, *p* = 0.014)	18				
Primary production (1-yr. lag)		0.362	0.138	0.019	0.225
SAM (Winter, 1-yr. lag)		-0.056	0.023	0.032	0.221
Calanus propinquus (r^2 = 0.71, *p* = <0.001)	18				
Primary production (1-yr. lag)		0.838	0.165	<0.001	0.553
Sea ice days (1-yr. lag)		-1.798	0.650	0.014	0.151

Table 2.5. Literature values (range) of total copepod and species abundance (ind. m^{-3}) for the dominant copepods in different regions of the Southern Ocean. Mean (maximum in parentheses) values from the present study (bolded) are included for comparison. Minimum values for present study are 0 ind. m^{-3}. 'AP' = Antarctic Peninsula.

Region	Season	Abundance (ind. m^{-3})									Reference
		Total copepods	*M. gerlachei*	*Oithona* spp.	*C. acutus*	Clauso-calanidae	*P. antarctica*	*Oncaea* spp.	*R. gigas*	*C. propinquus*	
WAP	**Summer**	**7 (67)**	**2 (16)**	**2 (49)**	**1 (43)**	**1 (11)**	**1 (4)**	**<1 (2)**	**<1 (2)**	**<1 (1)**	**This study**
NW AP; Bellingshausen Sea	Summer	7 - 846	<1 - 200	<1 - 150	<1 - 135	<1 - 45	<1 - 4	<1 - 4	<1-22	<1 - 1	a,b,c,d,e,f
Scotia Sea; South Georgia	Summer	-	5 - 144	8 - 526	4 - 31	<1 - 265	<1	1 - 21	<1 - 43	1	g,h
Prydz Bay; Weddell Sea	Summer	<1-10	<1 - 6	1 - 18	<1 - 11	<1 - 1	<1	<1 - 12	<1 - 8	<1 - 7	i,,j,k
Marguerite Bay	Autumn	28 - 46	2 - 44	<1 - 14	<1 - 95	<1 - 15	<1 - 8	<1 - 2	<1 - 1	<1 - 3	l

[a] Atkinson and Shreeve (1995)
[b] Huntley and Escritor (1991)
[c] Zmijewsja and Yen (1993)
[d] Cabal and Alvares-Marqués (2002)
[e] Calbet et al. (2005)
[f] Calbet et al. (2006)
[g] Ward et al. (2004)
[h] Ward et al. (2005)
[i] Kurbjeweit and Ali-Khan (1991)
[j] Li et al. (2001)
[k] Vuorinen et al. (1997)
[l] Marrari et al. (2011)

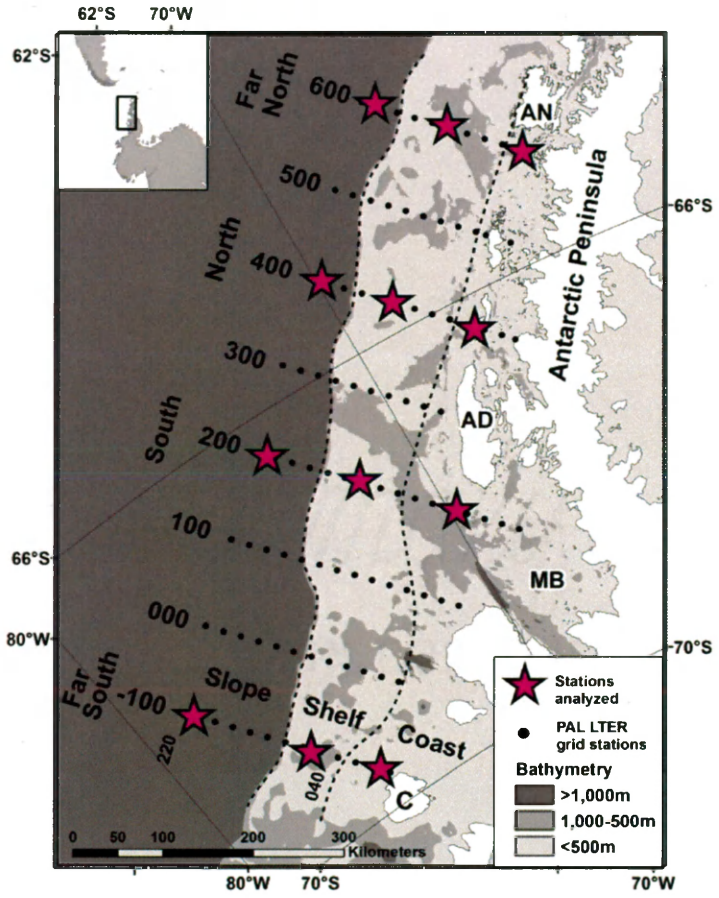
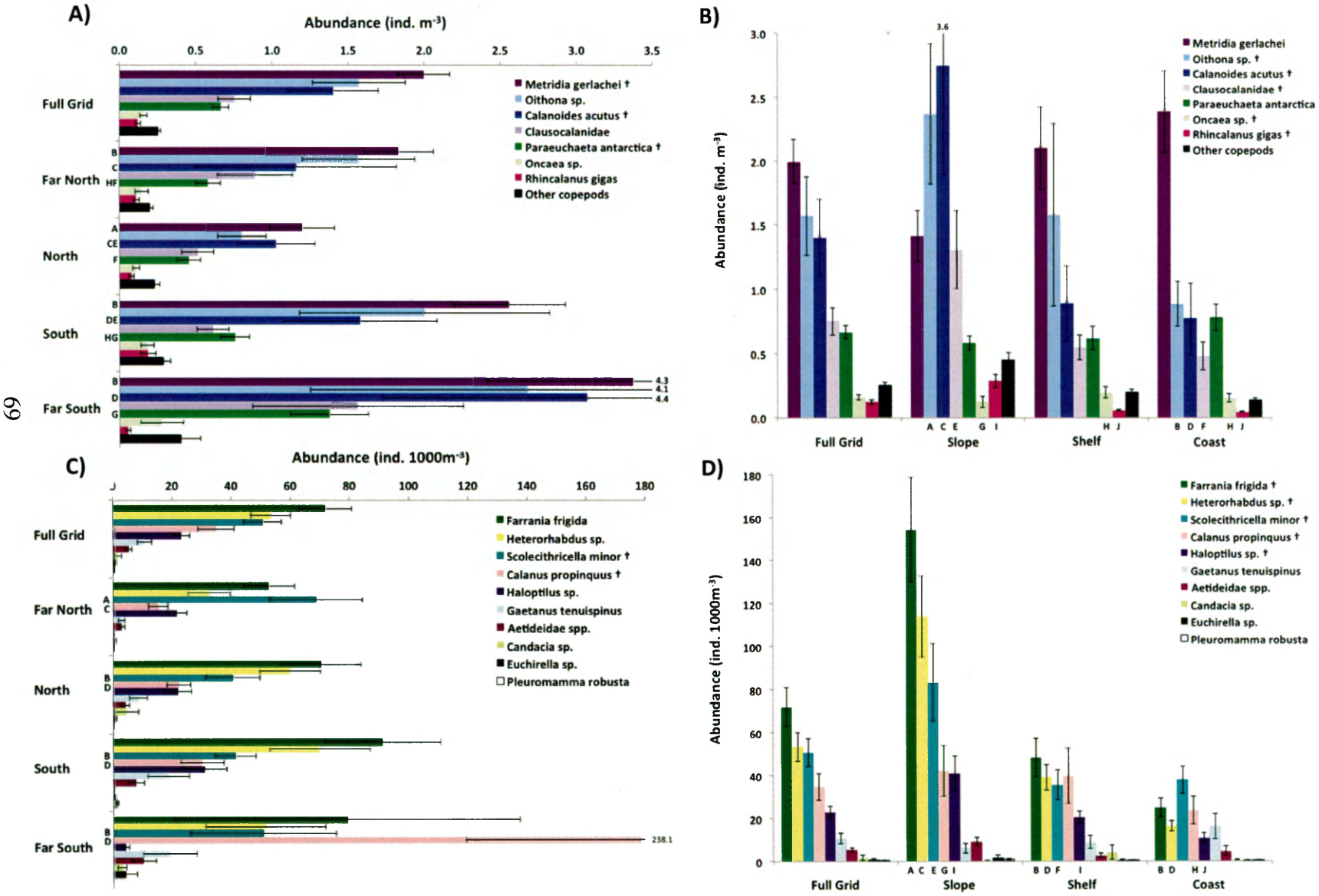


Figure 2.1. Stations sampled as part of the Palmer Long-Term Ecological Research (LTER) study off the Western Antarctic Peninsula. Stations included in our time-series analysis are indicated with a pink star. Study region, highlighted by box, in relation to Antarctic continent (inset). AN: Anvers Island, AD: Adelaide Island, MB: Marguerite Bay, C: Charcot Island. Palmer Station is located on Anvers Island. PAL LTER grid lines are numbered (600 to -100), and the far slope (220) and shelf (040) stations are indicated for reference (Waters & Smith 1992). 'Far north', 'north', 'south', and 'far south' sub-regions corresponding to gridline (600, 400, 200, -100) are indicated. Coast, shelf, and slope regions are separated by a dashed line. All region divisions are based on hydrographic and sea-ice conditions (Martinson et al. 2008, Stammerjohn et al. 2008a).

Figure 2.2. Mean abundance of copepods for the full PAL LTER grid area, and each latitudinal (A, C) and cross-shelf (B, D) sub-region. (A, B) are numerically dominant copepod species and (C, D) are rare copepods; note different x and y-axis scales. Mean abundance from tows collected from 1993-2013, with the exception of far south (2009-2013). Sample size for sub-regions are as follows: n = 201 (full grid), 65 (far north; FN), 58 (north; N), 62 (south; S), 16 (far south, FS), 60 (slope), 70 (shelf), 71 (coast). Error bars are standard error. † indicates a significant difference between latitudinal or cross-shelf sub-regions (Kurskal-Wallis test, $p < 0.05$). Copepod species abundance denoted by a different letter are significantly different between sub-regions (Rank Sum). Abundance of copepod species designated by the same letter (or no letter) are not significantly different between regions (Rank Sum). For example, *Calanoides acutus* abundance in latitudinal sub-regions (A) is significantly different between the FN vs. S, FN vs. FS, and N vs. FS, but there is no significant difference between FN vs. N, N vs. S, and S vs. FS.


A)
Abundance (ind. m-3)
0.0
0.5
1.0
1.5
2.0
2.5
3.0
3.5
Full Grid
Far North
North
South
Far South
Metridia gerlachei †
Oithona sp.
Calanoides acutus †
Clausocalanidae
Paraeuchaeta antarctica †
Oncaea sp.
Rhincalanus gigas
Other copepods
4.3
4.1
4.4
B)
Abundance (ind. m-3)
3.6
Full Grid
Slope
Shelf
Coast
Metridia gerlachei
Oithona sp. †
Calanoides acutus †
Clausocalanidae †
Paraeuchaeta antarctica
Oncaea sp. †
Rhincalanus gigas †
Other copepods
C)
Abundance (ind. 1000m-3)
Full Grid
Far North
North
South
Far South
Farrania frigida
Heterorhabdus sp.
Scolecithricella minor †
Calanus propinquus †
Haloptilus sp.
Gaetanus tenuispinus
Aetideidae spp.
Candacia sp.
Euchirella sp.
Pleuromamma robusta
238.1
D)
Abundance (ind. 1000m-3)
Full Grid
Slope
Shelf
Coast
Farrania frigida †
Heterorhabdus sp. †
Scolecithricella minor †
Calanus propinquus †
Haloptilus sp. †
Gaetanus tenuispinus
Aetideidae spp.
Candacia sp.
Euchirella sp.
Pleuromamma robusta

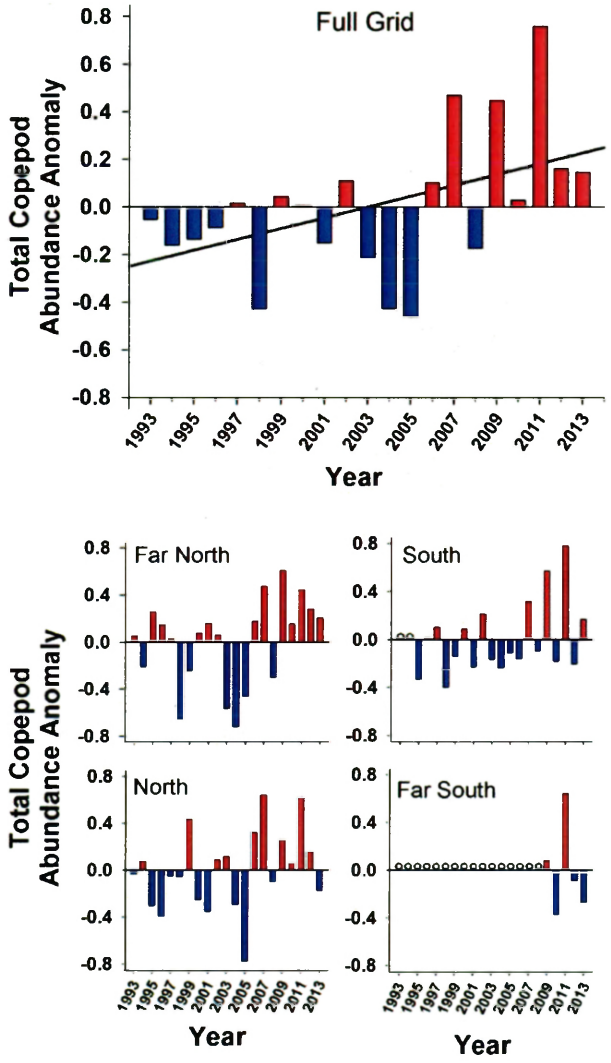


Figure 2.3. Annual abundance anomalies of total copepods. Upper plot is for the full grid area, and lower plots are latitudinal sub-regions. Open circles indicate no data that year. Regression line indicates significant linear relationship (Total copepods, full grid, $p = 0.031$, $r^2 = 0.22$).

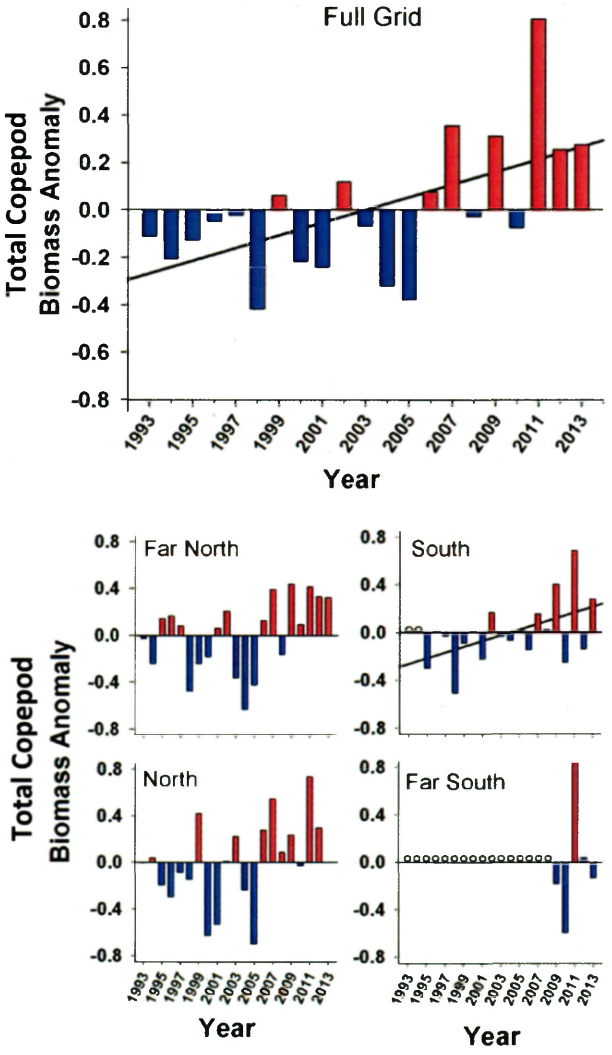
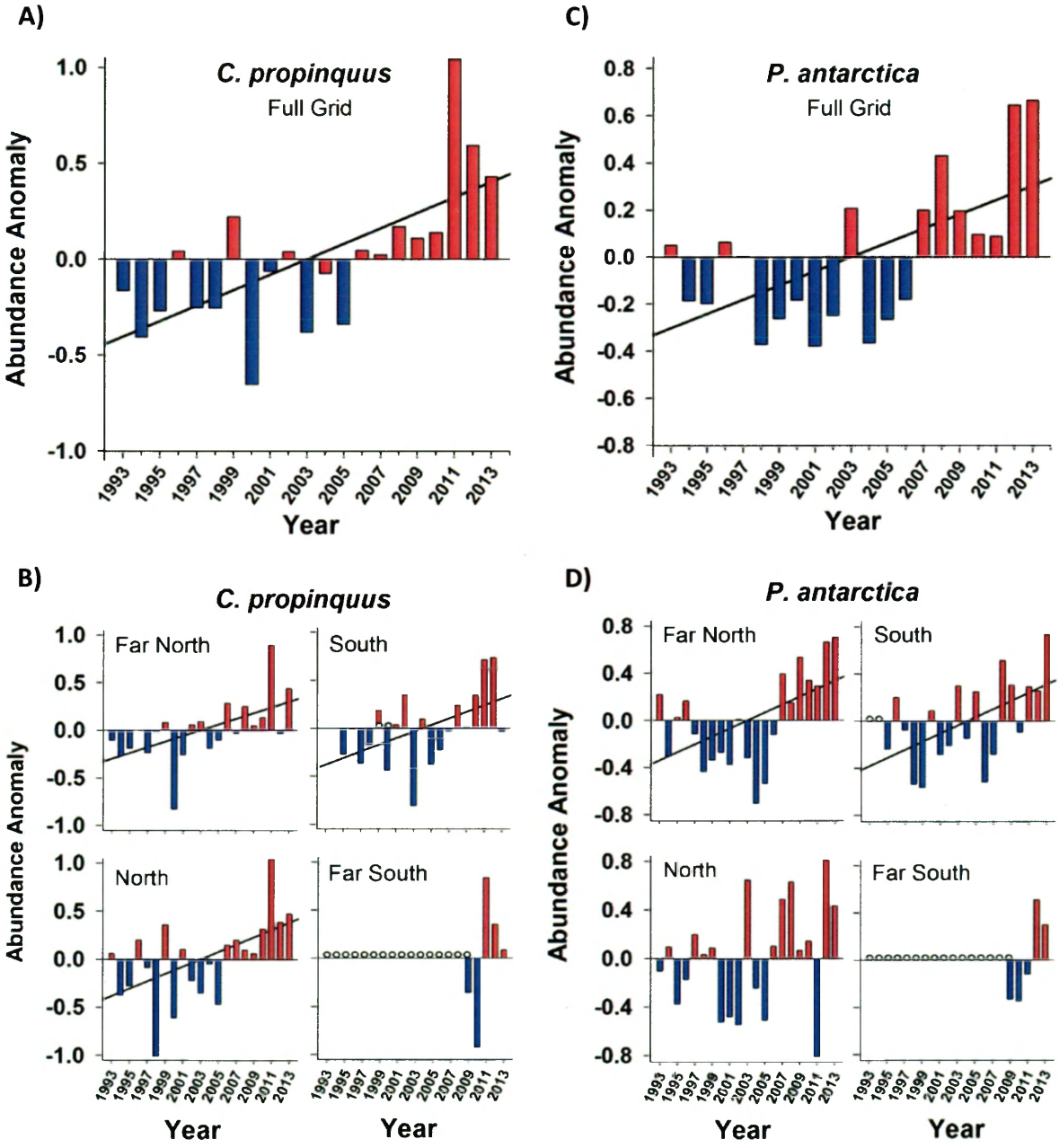


Figure 2.4. Annual biomass anomalies of total copepods. Upper plot is for the full grid area, and lower plots are latitudinal sub-regions. Open circles indicate no data that year. Regression line indicates significant linear relationship (Total copepods, full grid, $p = 0.006$, $r^2 = 0.33$; south, $p = 0.027$, $r^2 = 0.26$).

Figure 2.5. Annual abundance anomaly of the copepods A, B) *Calanus propinquus* and C, D) *Paraeuchaeta antarctica.* A and C (upper plots) are for the full grid area; B and D (lower plots) are latitudinal sub-regions. Open circles indicate no data that year. Regression lines indicate significant linear relationships. A) *C. propinquus,* full grid, $p = <0.001$, $r^2 = 0.44$. B) *C. propinquus*, far north, $p = 0.007$, $r^2 = 0.32$; north, $p = 0.011$, $r^2 = 0.29$; south, $p = 0.028$, $r^2 = 0.25$. C) *P. antarctica*, full grid, $p = 0.004$, $r^2 = 0.36$. D) *P. antarctica,* far north, $p = 0.015$, $r^2 = 0.28$; south, $p = 0.019$, $r^2 = 0.23$.


A)
C. propinquus
Full Grid
Abundance Anomaly
Year
C)
P. antarctica
Full Grid
Abundance Anomaly
Year
B)
C. propinquus
Far North
South
North
Far South
Abundance Anomaly
Year
D)
P. antarctica
Far North
South
North
Far South
Abundance Anomaly
Year

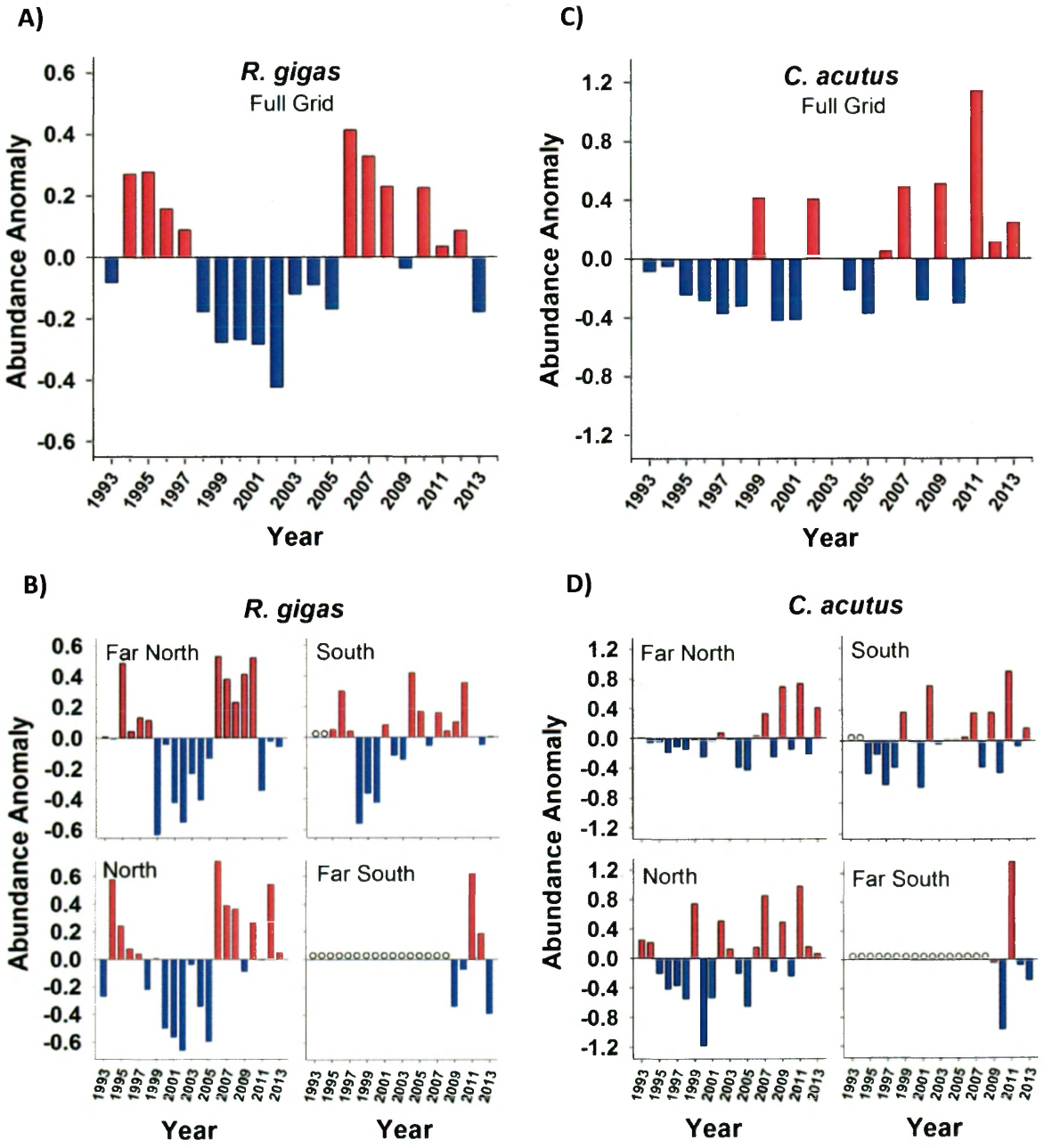


Figure 2.6. Annual abundance anomaly for copepods A,B) *Rhincalanus gigas* and C,D) *Calanoides acutus*. A and C (upper plots) are for the full grid area; B and D (lower plots) are latitudinal sub-regions. Open circles indicate no data that year.

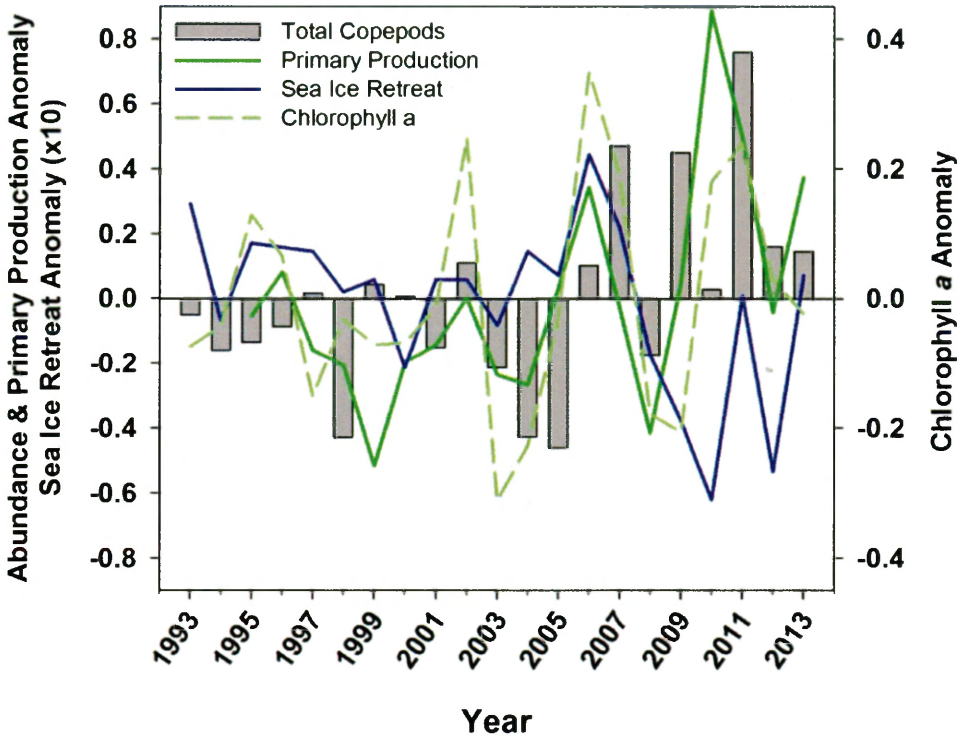
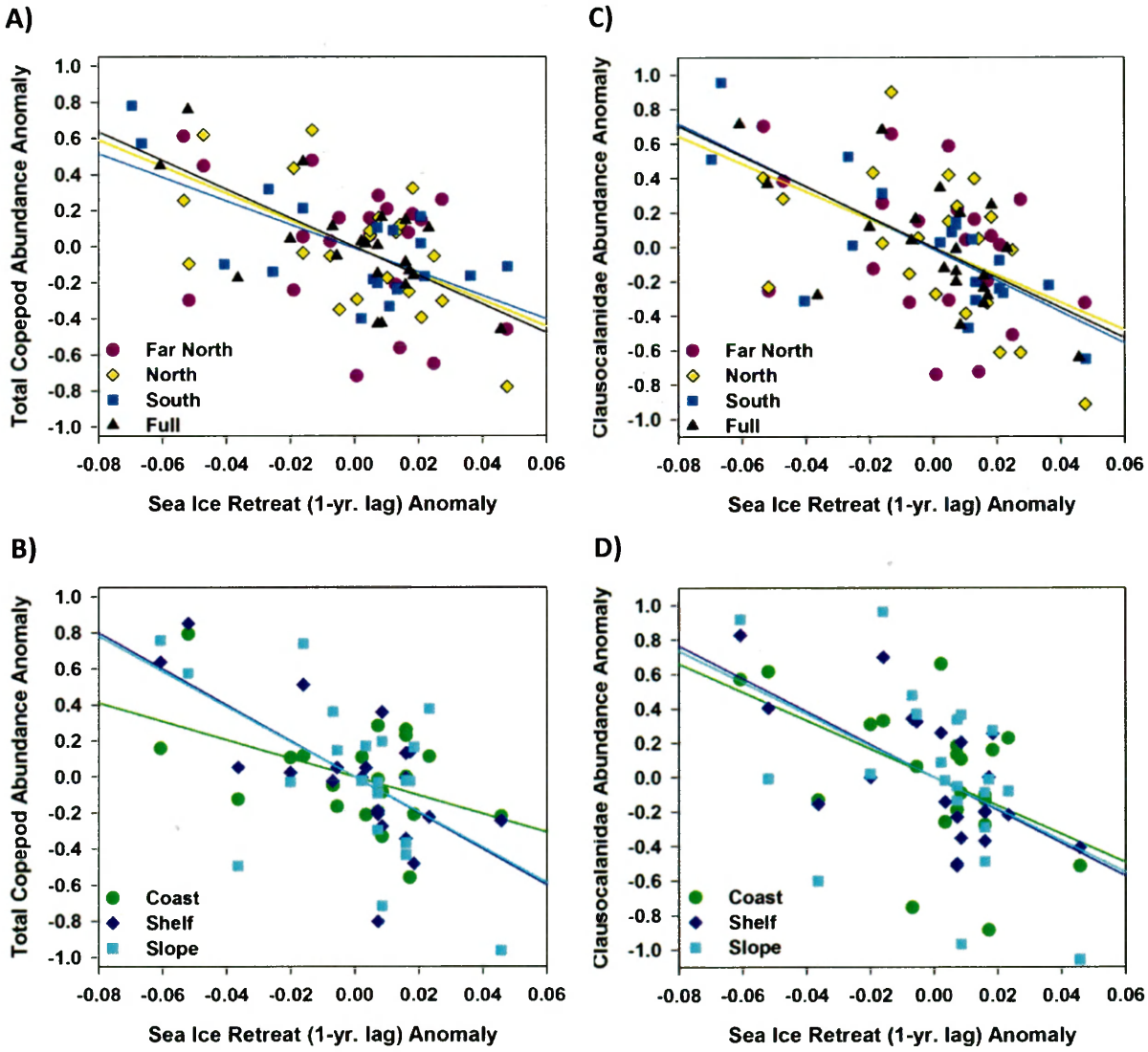


Figure 2.7. Annual abundance anomaly of total copepods and environmental variables. Anomalies and linear regressions are for the full grid area. Negative sea ice retreat anomaly indicates an earlier retreat and positive anomaly indicates later retreat. Primary production (1-yr. lag), $p = 0.012$, $r^2 = 0.33$, $n = 18$. Sea ice retreat, $p = 0.001$, $r^2 = 0.45$. $n = 21$. Chlorophyll *a* (0-yr. lag), $p = 0.047$, $r^2 = 0.19$, $n = 21$. Primary production (0-yr. lag) does not have a significant linear regression with total copepod abundance anomaly. Note y-axis values listed are 10 times greater than sea ice retreat anomaly.

Figure 2.8. Relationship between sea ice retreat and (A, B) total copepod abundance and (C, D) Clausocalanidae abundance. Data plotted are annual abundance anomalies for each year of the time series (1993-2013) for indicated regions. Negative sea ice retreat anomaly indicates an earlier retreat and positive anomaly indicates later retreat. Regression lines for significant linear relationships are shown. A) Total copepods, north, $p = 0.008$, $r^2 = 0.32$; south, $p = 0.001$, $r^2 = 0.47$; full grid, $p = 0.001$, $r^2 = 0.45$. B) Total copepods, coast, $p = 0.033$, $r^2 = 0.22$; shelf, $p = 0.001$, $r^2 = 0.45$; slope, $p = 0.009$, $r^2 = 0.31$. C) Clausocalanidae, north, $p = 0.023$, $r^2 = 0.25$; south, $p = <0.001$, $r^2 = 0.57$; full grid, $p = <0.001$, $r^2 = 0.41$. D) Clausocalanidae, coast, $p = 0.018$, $r^2 = 0.26$; shelf, $p = 0.002$, $r^2 = 0.40$; slope, $p = 0.038$, $r^2 = 0.21$.


A)
C)
B)
D)
Total Copepod Abundance Anomaly
Clausocalanidae Abundance Anomaly
Sea Ice Retreat (1-yr. lag) Anomaly
Far North
North
South
Full
Coast
Shelf
Slope
1.0
0.8
0.6
0.4
0.2
0.0
-0.2
-0.4
-0.6
-0.8
-1.0
-0.08
-0.06
-0.04
-0.02
0.00
0.02
0.04
0.06

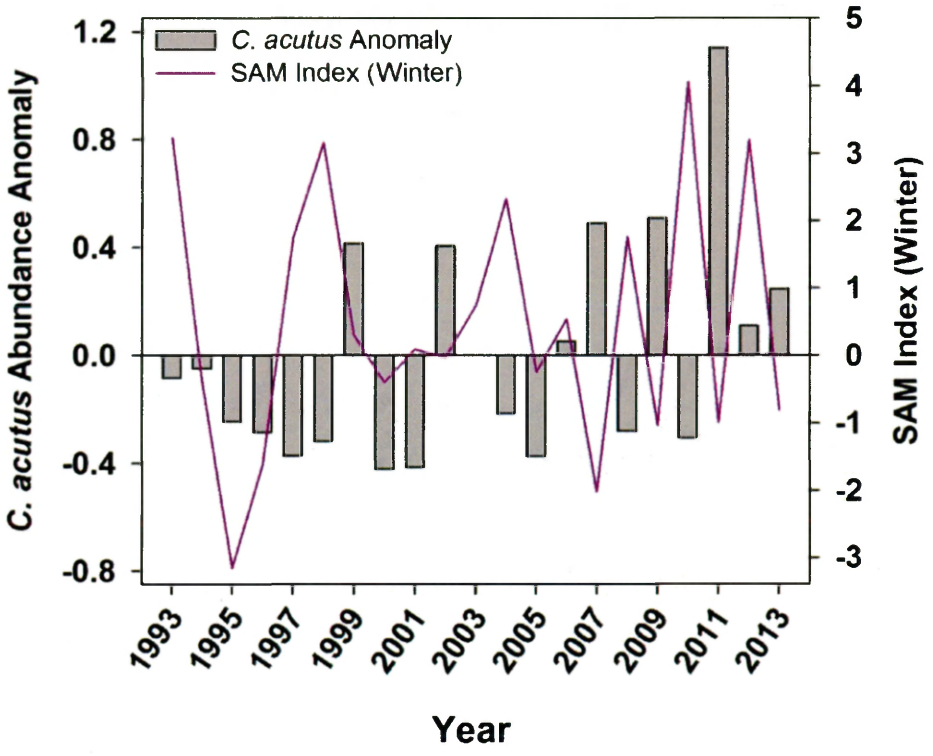
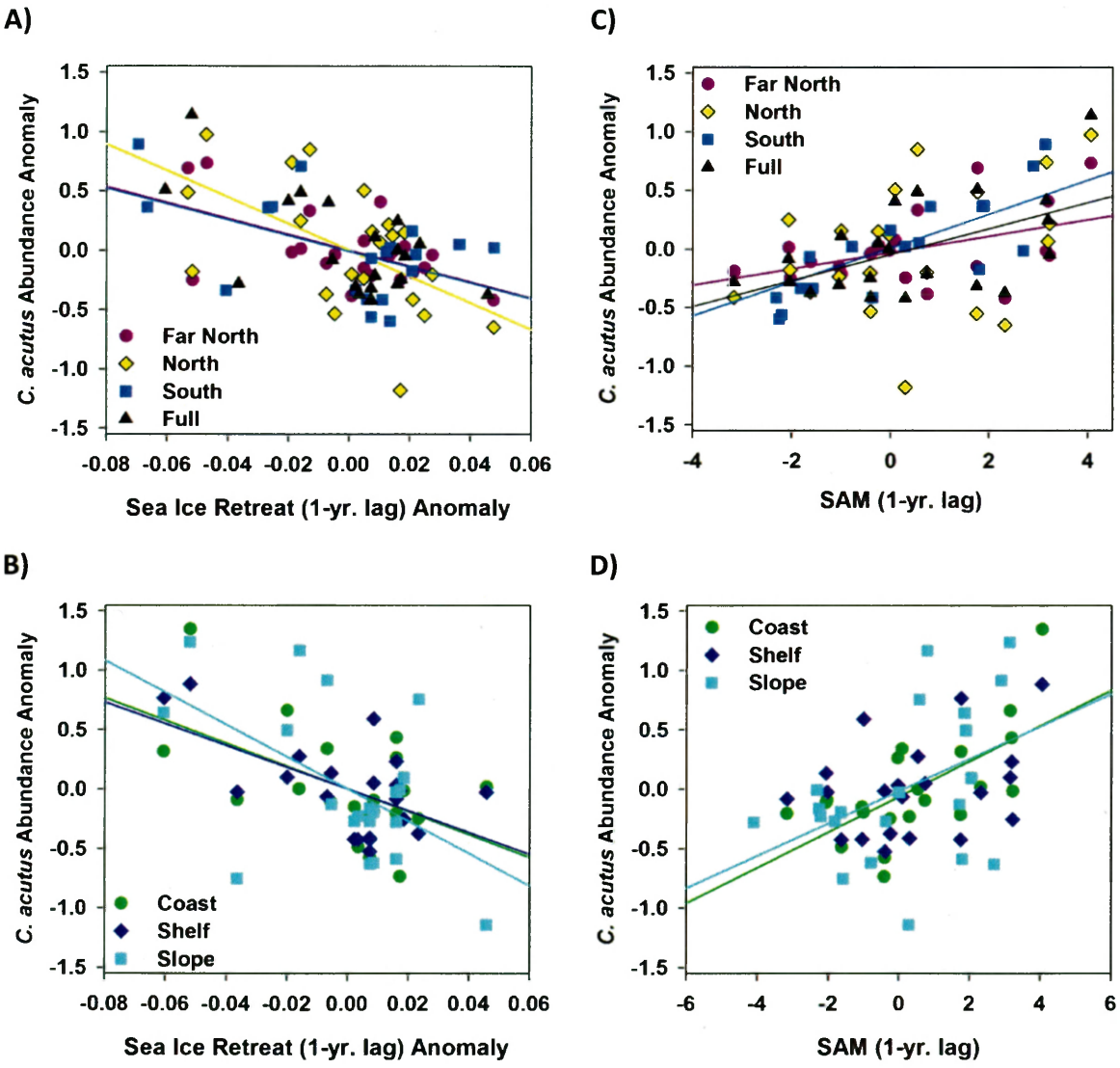


Figure 2.9. Annual abundance anomaly of *Calanoides acutus* and Southern Annular Mode (SAM) Index. Anomalies and significant linear regression are for the full grid area. SAM Index (Winter, 1-yr. lag), $p = 0.011$, $r^2 = 0.29$, $n = 21$.

Figure 2.10. Effect of sea ice retreat and Southern Annular Mode (SAM) Index on abundance of copepod *Calanoides acutus*. Data plotted are annual abundance anomalies for each year of the time series (1993-2013) for indicated regions. Negative sea ice retreat anomaly indicates an earlier retreat and positive anomaly indicates later retreat. Regression lines for significant linear relationships are shown. A) Sea ice retreat (1-yr. lag), far north, $p = 0.007$, $r^2 = 0.33$; north, $p = 0.01$, $r^2 = 0.30$; south, $p = 0.023$, $r^2 = 0.27$; full grid, p 0.002, $r^2 = 0.41$. B) Sea ice retreat (1-yr. lag), coast, $p = 0.013$, $r^2 = 0.29$; shelf, $p = 0.005$, $r^2 = 0.35$; slope, $p = 0.013$, $r^2 = 0.28$. C) SAM Index (1-yr. lag), far north, $p = 0.04$, $r^2 = 0.20$; south, $p < 0.001$, $r^2 = 0.54$; full grid, $p = 0.011$, $r^2 = 0.29$. D) SAM Index (1-yr. lag), coast, $p = 0.001$, $r^2 = 0.43$; slope, $p = 0.049$, $r^2 = 0.19$.


A)
C)
B)
D)
C. acutus Abundance Anomaly
Sea Ice Retreat (1-yr. lag) Anomaly
SAM (1-yr. lag)
Far North
North
South
Full
Coast
Shelf
Slope
1.5
1.0
0.5
0.0
-0.5
-1.0
-1.5
-0.08 -0.06 -0.04 -0.02 0.00 0.02 0.04 0.06
-4 -2 0 2 4
-6 -4 -2 0 2 4 6

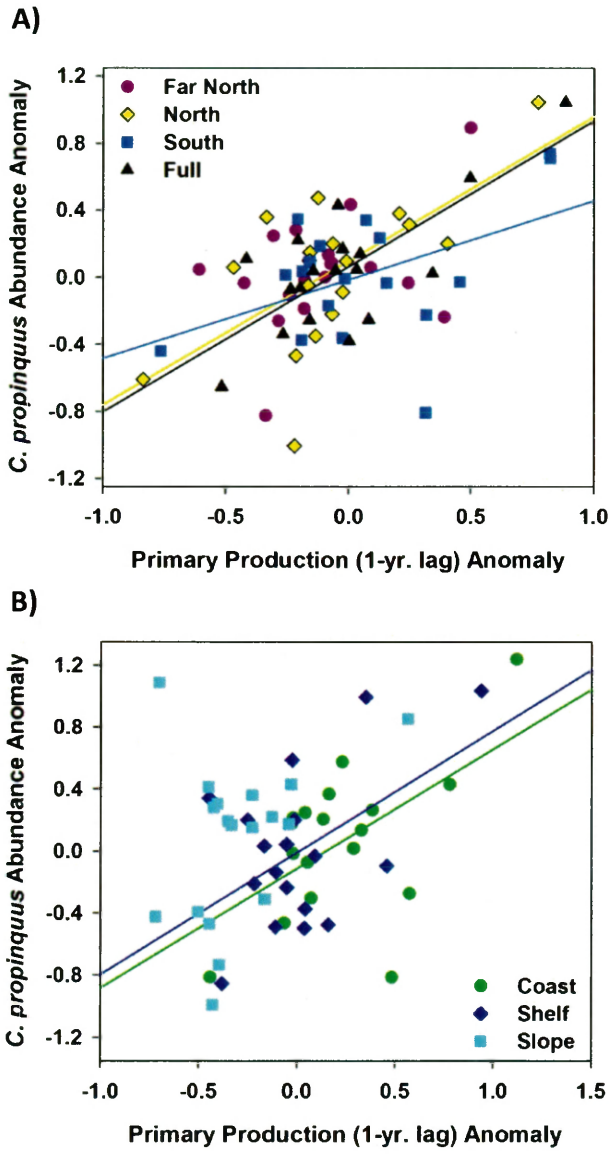


Figure 2.11. Relationship between primary production (1-yr. lag) and abundance of copepod *Calanus propinquus*. Data plotted are annual abundance anomalies for each year of the time series (1993-2013) for indicated regions. Regression lines for significant linear relationships are shown. A) Primary production (1-yr. lag), north, $p = 0.004$, $r^2 = 0.42$; south, $p = 0.05$, $r^2 = 0.22$; full grid, $p = <0.001$, $r^2 = 0.55$. B) Primary production (1-yr. lag), coast, $p = 0.016$, $r^2 = 0.31$; shelf, $p = 0.034$, $r^2 = 0.25$.

Figure 2.12. Principle component analysis (PCA) for the dominant copepod species and environmental variables/climate indices for the time series (1993-2013). Data used for copepod species and environmental variables (sea ice, primary production) are annual anomalies for each year of the time series. A) full grid area, and latitudinal sub-regions, B) far north, and C) south. Copepod species are: Clausocalanidae ('C'), *Calanoides acutus* ('C.a.'), *Calanus propinquus*, ('C.p.'), *Metridia gerlachei* ('M.g.'), *Oithona* spp. ('Oi'), *Oncaea* spp. ('On'), *Paraeuchaeta antarctica* ('P.a.'), *Rhincalanus gigas* ('R.g.'). Environmental parameters are: sea ice retreat (1-yr. lag), primary production (0-yr. lag), and primary production (1-yr. lag). Sea ice retreat in A) is an average of the full grid area, in B) measured at Anvers Island in the far north, and C) Avian Island in the south. Primary production in A) is for the full grid area, and B) and C) are sub-region means. Climate index is Southern Annual Mode (SAM; 1-yr. lag).

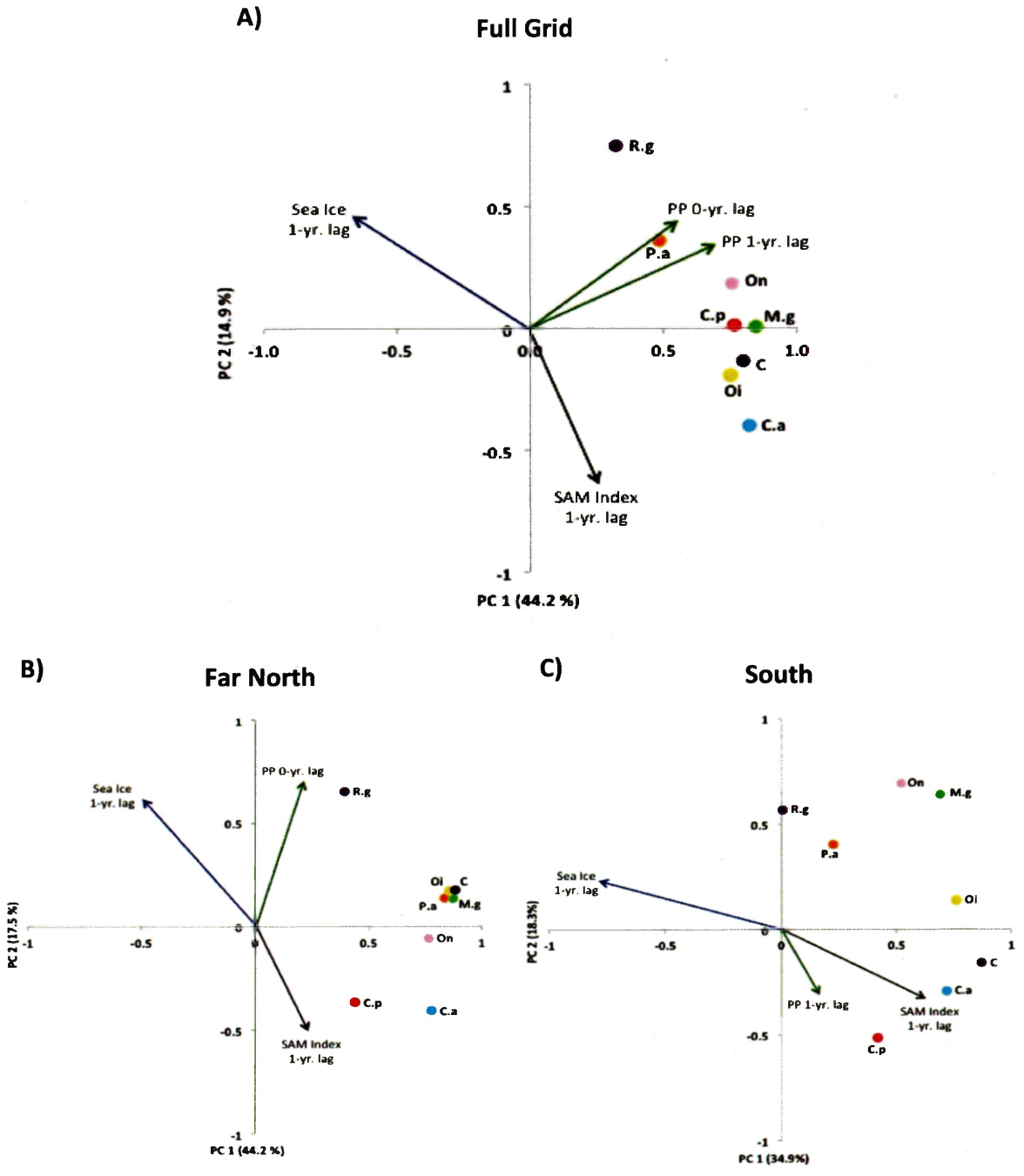
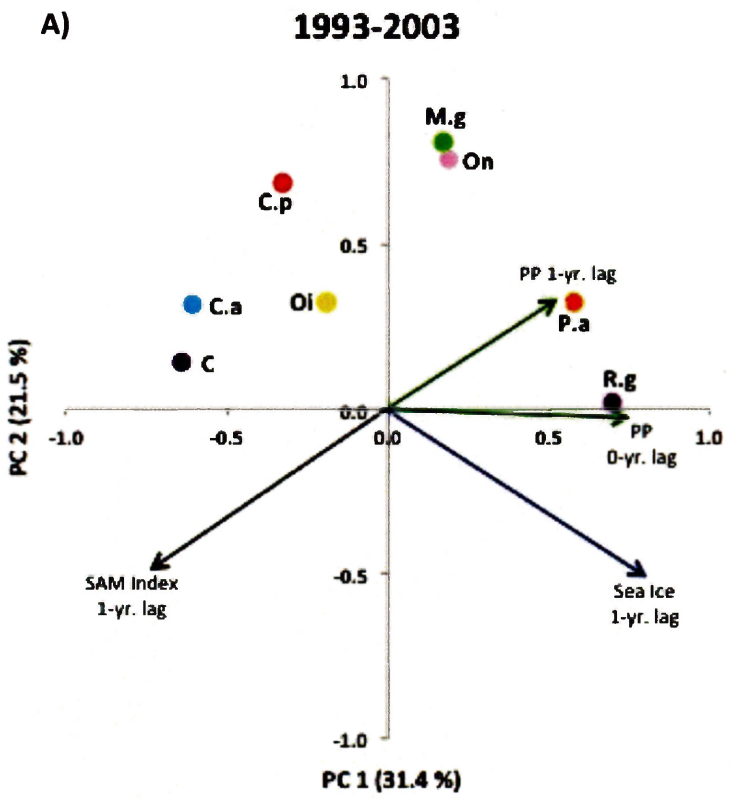
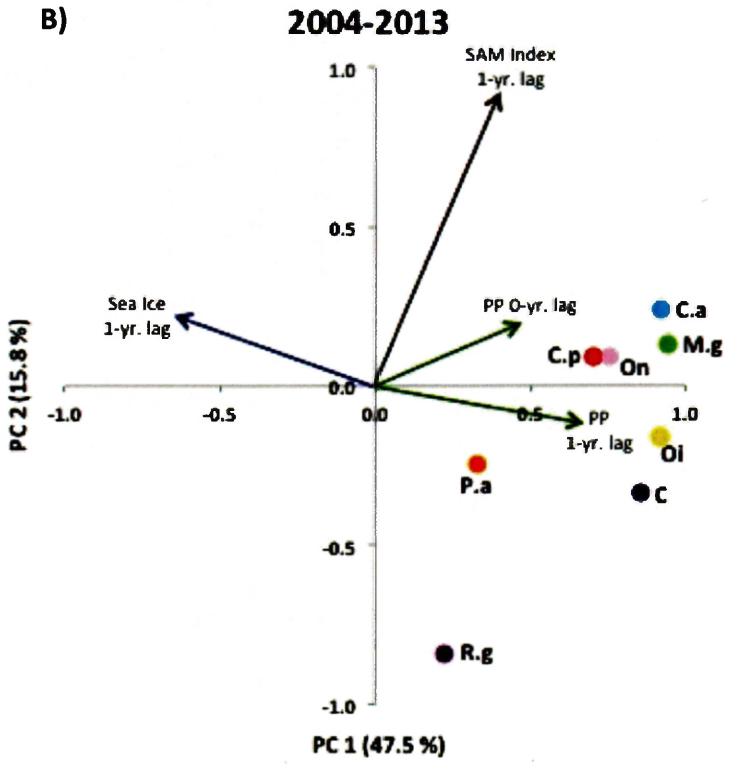

A)
Full Grid
R.g
Sea Ice
1-yr. lag
PP 0-yr. lag
P.a
PP 1-yr. lag
On
C.p
M.g
C
Oi
C.a
SAM Index
1-yr. lag
PC 2 (14.9 %)
PC 1 (44.2 %)
B)
Far North
PC 2 (17.5 %)
PC 1 (44.2 %)
C)
South
PC 2 (18.3%)
PC 1 (34.9%)

Figure 2.13. Principle component analysis (PCA) for the dominant copepod species and environmental variables/climate indices for A) the first half of the time series (1993-2003), and B) second half of the time series (2004-2013). Data used for copepod species and environmental variables (sea ice, primary production) are annual anomalies for each year of the full time series. Copepod species are: Clausocalanidae ('C'), *Calanoides acutus* ('C.a.'), *Calanus propinquus*, ('C.p.'), *Metridia gerlachei* ('M.g.'), *Oithona* spp. ('Oi'), *Oncaea* spp. ('On'), *Paraeuchaeta antarctica* ('P.a.'), *Rhincalanus gigas* ('R.g.'). Environmental parameters are: sea ice retreat (1-yr. lag), primary production (0-yr. lag), and primary production (1-yr. lag). Sea ice retreat and primary production are full grid area mean. Climate index is Southern Annual Mode (SAM; 1-yr. lag).


A)
1993-2003
1.0
0.5
0.0
-0.5
-1.0
-1.0
-0.5
0.0
0.5
1.0
M.g
On
C.p
C.a
Oi
C
PP 1-yr. lag
P.a
R.g
PP
0-yr. lag
SAM Index
1-yr. lag
Sea Ice
1-yr. lag
PC 2 (21.5 %)
PC 1 (31.4 %)


B)
2004-2013
1.0
0.5
0.0
-0.5
-1.0
-1.0
-0.5
0.0
0.5
1.0
SAM Index
1-yr. lag
Sea Ice
1-yr. lag
PP 0-yr. lag
C.a
M.g
C.p
On
PP
1-yr. lag
Oi
P.a
C
R.g
PC 2 (15.8 %)
PC 1 (47.5 %)

CHAPTER 3

Copepod grazing impact and fecal pellet production along the Western Antarctic Peninsula

ABSTRACT

Copepods are important grazers on phytoplankton and contributors to carbon export through production of fecal pellets, but their impact on both is not well known throughout much of the Western Antarctic Peninsula (WAP), a region of rapid climate warming. We conducted grazing (gut fluorescence method), and fecal pellet production experiments with copepods in the WAP each January from 2012 to 2014 as part of the Palmer Antarctica Long-Term Ecological Research (PAL LTER) program. Mean gut evacuation rates (k) for *Calanus propinquus* (0.61 h^{-1}), *Rhincalanus gigas* (0.63 h^{-1}), and *Calanoides acutus* (0.37 h^{-1}), and mean initial gut content (G) for *C. propinquus* (8.4 ng {Chl *a* equiv.} $ind.^{-1}$), *R. gigas* (10.7 ng {Chl *a* equiv.} $ind.^{-1}$), and *C. acutus* (4.3 ng {Chl *a* equiv.} $ind.^{-1}$) resulted in high ingestion rates (I) for *C. propinquus* and *R. gigas* (133 ng {Chl *a* equiv.} $ind.^{-1}$ day^{-1}), and lower for *C. acutus* (37 ng {Chl *a* equiv.} $ind.^{-1}$ day^{-1}). Since k and I linearly increased with increasing chlorophyll *a* for most species, ingestion rates were 4-70 times greater in the more productive coastal region than in offshore, slope waters. Fecal pellet production (egestion) rates ranged from 0.82 (*R. gigas)* to 37.3 µgC ind. day^{-1} (*Paraeuchaeta antarctica).* Using January 1993-2013 copepod abundance data we found copepods have a low overall grazing impact on phytoplankton biomass (<1%) and productivity (1%, but up to 11%), which is at the low end of grazing impact compared to the dominant macrozooplankton in the region. Copepods were likely feeding on other sources of carbon (i.e., protozoans and metazoans) to meet metabolic demands, especially on the slope and in low chl *a*

conditions, where copepods ingested <0.3% of their body carbon content from phytoplankton. In comparison, body C rations from phytoplankton were on average 1.2 – 3.3% (up to 13%) during a large coastal phytoplankton bloom in 2014, indicating changes in chl *a* and productivity impact copepod reliance on phytoplankton compared to other food sources. Future changes in the WAP plankton community may affect flow of carbon through the food web and export to depth.

1. INTRODUCTION

In the Southern Ocean copepods are the most abundant mesozooplankton taxa, and are important grazers of phytoplankton– with daily carbon ingestion up to 50% of primary production (Schnack-Schiel et al. 1985, Conover & Huntley 1991, Atkinson & Shreeve 1995, Atkinson et al. 1996a, Dubischar & Bathmann 1997, Cabal & Alvarez-Marqués 2002, Mayzaud et al. 2002). The dominant Southern Ocean copepods employ feeding modes ranging from carnivorous (*Paraeuchaeta antarctica*), to omnivorous (*Calanus propinquus*), to mostly herbivorous (*Calanoides acutus*) (Yen 1991, Atkinson 1998, Pasternak & Schnack-Schiel 2001a), but most have flexible feeding behaviors depending on food availability (Atkinson 1994, 1995, 1998; Metz & Schnack-Schiel 1995; Froneman & Pakhomov 1996; Calbet et al. 2006). Furthermore, larger copepods produce carbon-rich fecal pellets with sinking rates of 100's m day^{-1} that can be important source of carbon export from the euphotic zone (Turner 2002, Dubischar & Bathmann 2002, Dagg et al. 2003, Gleiber et al. 2012). In a 5-year time-series analysis of sediment trap collections over the continental shelf of the Western Antarctic Peninsula (WAP), copepods had the second highest contribution to carbon flux from fecal pellets by taxon (after krill), contributing an annual average of 22% of the total fecal pellet POC flux (compared to 72% for krill fecal pellets; Gleiber et al. 2012). Thus, copepods are both important grazers and mediators of C flux.

The WAP has some of the highest seasonal productivity in the Southern Ocean (Ducklow et al. 2012), and is experiencing one of the most rapid rates of warming on Earth (Vaughan et al. 2003). The close proximity of the Antarctic Circumpolar Current (ACC) facilitates delivery of Upper Circumpolar Deep Water (UCDW) onto the continental shelf; water that is both nutrient rich and relatively warm (Martinson et al. 2008). A large summer phytoplankton bloom (over 600 mg Chl *a* m^{-2}) supports a marine ecosystem with high abundance of krill that are food for upper trophic levels, such as seabirds and marine mammals (Ducklow et al. 2012). Changes due to warming in the northern WAP over the last few decades have led to a latitudinal 'climate gradient', affecting food web dynamics with significant changes at all trophic levels from plankton to top-predators (Ducklow et al. 2007, 2012; Montes-Hugo et al. 2008; Stammerjohn et al. 2008).

Krill and other macrozooplankton in summer in the WAP have a low average grazing impact (<1% of daily primary production), although localized krill swarms and ephemeral salp blooms can consume over 100% of primary production (Bernard et al. 2012). A recent study by Garzio et al. (2013) found microzooplankton (<200 µm, mostly single-celled protozoa) are important grazers in the WAP, consuming 32 - >100% of PP, and that they exert higher grazing pressure on bacterioplankton, picoautotrophs, and nanophytoplankton than on large diatoms (>20µm) that dominate the summer blooms (Montes-Hugo et al. 2008, 2010). An inverse-model for the WAP food web further indicates a shift over the last decade in the northern WAP from an herbivorous system, with krill as the dominant grazers, to a microbial system where microzooplankton are the dominant grazers (Sailley et al. 2013). With their flexible feeding strategies, copepods are

a direct link between these two systems, as possible grazers of both large diatoms and microzooplankton. The role of copepods in affecting the fate of the WAP summer phytoplankton bloom, however, is largely unknown.

Time-series analysis indicates changes are occurring in WAP zooplankton (Ross et al. 2008, Steinberg et al. in review), including increasing copepod abundance over the past two decades (Chapter 2). Long-term changes in zooplankton can lead to changes in the efficiency of the biological pump and impact higher trophic levels (Steinberg et al. 2012a). This study aims to investigate the role of copepods in grazing of phytoplankton and in fecal pellet production in the WAP. By further understanding the importance of copepods in carbon and energy transfer in the pelagic food web and biogeochemical cycling in the WAP, we can gain a more comprehensive understanding of the effects of climate change in this region.

2. MATERIALS AND METHODS

2.1 Study area and copepod collection

We conducted experiments to examine grazing and egestion (fecal pellet production) rates for the large, dominant copepod species in the western Antarctic Peninsula (WAP) in January 2012, 2013, and 2014 aboard the *ARSV Laurence M. Gould* during the annual Palmer Antarctica Long-Term Ecological Research (PAL LTER) cruise. The PAL LTER samples a grid of stations encompassing north-south, and coastal-shelf-slope gradients along the WAP (Figure 3.1; Martinson et al. 2008, Ducklow et al. 2012).

Copepods were collected at stations throughout the PAL LTER grid (Ducklow et al. 2012) in double oblique net tows within the upper 200 m using a 2 x 2 m rectangular frame net with 700 µm mesh and non-filtering cod end (see Appendix 1 and 2 for sampling location details). Precautions were taken to limit gut evacuation during sampling, including low towing speed and short (< 20 min.) tow duration (Båmstedt et al. 2000). Preliminary sampling indicated the 2 x 2 m, 700 µm mesh net caught copepods in better condition than a 1 x 1 m, 333 µm mesh net also used as part of the sampling to target copepods and smaller zooplankton. In this study we focus on the larger (>1mm) adult copepods of *Calanoides acutus, Calanus propinquus, Rhincalanus gigas,* and *Paraeuchaeta antarctica.* We acknowledge that small copepods (e.g., *Metridia gerlachei*,

Oithona sp., Clausocalanidae, *Oncaea* sp.) are also abundant in the region (Chapter 2) and include available literature values for these species in our calculations of total copepod grazing (see *Section 2.2*).

Phytoplankton biomass and primary production were determined at each station at discrete depths (see Vernet et al. 2008) and integrated as described in Bernard et al. (2012). Phytoplankton biomass (mg Chl *a* m^{-2}) was integrated over the top 100m of the water column and primary production (mg C m^{-2} day^{-1}) integrated to the bottom of the euphotic zone (30-70m).

2.2 Grazing rate analysis and integrated grazing calculations

Grazing rates were estimated using the gut fluorescence analysis technique described by Båmstedt et al. (2000), but omitting the gut pigment degradation correction since this is already taken into account with the exponential evacuation rate curve in gut evacuation rate experiments (Durbin & Campbell 2007, Landry et al. 2009, Bernard et al. 2012). Ingestion rates were calculated for each copepod species as in Bernard et al. (2012) using equations derived in Båmstedt et al. (2000):

$$I = k \times G$$

where I is ingestion rate [ng (Chl-*a* equivalent) $ind.^{-1}$ day^{-1}], G is instantaneous gut pigment content [ng (Chl-*a* equivalent) $ind.^{-1}$], and k is daily gut evacuation rate (day^{-1}). Methods for measuring instantaneous gut pigment content and gut evacuation rate are described below.

Daily integrated grazing rates for individual copepod species were estimated using measured abundances for each species over the entire 21-year PAL LTER time

series (Chapter 2). We calculated a grazing rate for each species as the product of ingestion rate (see *Section 3.2.2*) and integrated abundance (ind. m^{-2}) enumerated from 1x1m, 333 µm mesh net 0-300m oblique tows collected in January 1993 – 2013 (n = 202; Båmstedt et al. 2000):

$$\text{Integrated grazing rate [µg (Chl-}a\text{ equiv.) m}^{-2}\text{ day}^{-1}\text{]} = \text{I} \times \text{Abundance (ind. m}^{-2}\text{)}$$

The integrated grazing rate for total copepods was calculated as the sum of species grazing rates calculated (see above) for each tow, multiplied by the integrated abundance of each species.

Integrated grazing rates were converted to carbon using a Carbon: Chl-*a* ratio of 63:1 (Bernard et al. 2012). These values were used to estimate copepod grazing impact on phytoplankton biomass (mg Chl *a* m^{-2}) and primary production (mg C m^{-2} day^{-1}) by species and for the whole copepod community.

2.2.1 Instantaneous gut content pigment analysis (G)

For measurement of instantaneous gut pigment content, copepods (*C. acutus, C. propinquus*, *R. gigas*, and *M. gerlachei*) were collected (Figure 3.1, Appendix 1). Copepods were removed from the cod end and immediately anesthetized with soda water (Kleppel et al. 1988, Båmstedt et al. 2000) to prevent gut clearance during sorting procedures. Copepod species were visually identified, transferred to cryovials (1-20 copepods of same species per cryovial), immediately frozen in liquid nitrogen, and stored at -80°C for gut fluorescence analysis (*Section 2.2.3*). Due to potential pigment

degradation from light exposure, all sorting took place as rapidly as possible in dim light conditions (Morales et al. 1990).

2.2.2 Gut evacuation rate (GER) experiments (k)

Two replicate gut evacuation rate (GER) experiments were conducted at sites located near Anvers and Avian Islands during 2-3 day 'process studies'. Additional experiments were conducted near Charcot Island in January 2012 and 2013, at slope (offshore) stations 600.200 in January 2013, and 100.160 in January 2014 (Figure 3.1, Appendix 1). The total number of experiments for all three years combined for each species is as follows: *C. acutus* (n=27), *C. propinquus* (n=23), *R. gigas* (n=23). We do not consider *P. antarctica*, a carnivorous copepod (Yen 1991).

For GER experiments, contents of the cod end were gently transferred to a 20-L bucket containing surface seawater through a submerged 5 mm mesh sieve–to remove krill and other large zooplankton, while minimizing damage to copepods. Copepods were immediately transferred with a 0.5 mm mesh sieve (mesh size excludes large phytoplankton) to replicate 20-L buckets containing particle-free seawater (0.2 μm filtered). Buckets were placed in a flow-through aquarium tank maintained at ±1.0°C ambient temperature for the duration of the experiments. The first time point (t=0) was taken 3-10 minutes after the cod end was recovered. Subsequent samples were taken at t=5, 10, 15, 20, 25, 30, 40, 50, 60, 90, 120, and 180 minutes (Dubischar & Bathmann 1997, Froneman et al. 2000, Pakhomov & Froneman 2004b). At each time point copepod sub-samples were removed from each replicate bucket using a 0.5 mm mesh sieve and immediately anesthetized with soda water (Kleppel et al. 1988, Båmstedt et al. 2000) to

prevent gut clearance during sorting. Due to gut pigment degradation from light exposure, all sorting took place as quickly as possible in dim light conditions (Morales et al. 1990, Båmstedt et al. 2000). Sorting at each time point took 5-10 minutes, and samples were stored in a dark refrigerator at -0.1 °C prior to sorting. Copepod species were identified, transferred to cryovials (1-20 copepods of same species per cryovial), immediately frozen in liquid nitrogen, and stored at -80°C for gut fluorescence analysis (*Section 2.2.3*).

Gut evacuation rate constants (k, hour^{-1}) were calculated as the slope of the exponential decrease of gut pigments G (chl a + phaeopigments) over time (Båmstedt et al. 2000, Bernard et al. 2012). We compared gut evacuation rates calculated with an exponential and linear model with variability in the ending time (t = 1.0, 1.5, 2.0, 3.0 hours) (Schnetzer and Steinberg 2002). An exponential model with experiments conducted over 3 hours fit best (i.e., highest r^2) the decline of gut pigments during the GER experiments. Gut passage times were then calculated from $1/k$ (hours). Hourly gut evacuation rates (k) were multiplied by 24 to convert to daily gut evacuation rates, k (day^{-1}), and used in the ingestion rate equation (see *Section 2.2*).

2.2.3 Gut fluorescence analysis

Gut contents of copepods were determined fluorometrically before and after acidification as described in Båmstedt et al. (2000). For analysis of January 2012 gut pigments, 1-2 replicate groups of copepods of each species (25-75 for *C. acutus*, 5-25 for *C. propinquus*, and 1-2 for *R. gigas* and *P. antarctica)* were homogenized with a Misonix XL-2000 sonicator in 10 mL of 90% acetone. Gut pigments were extracted in a freezer

for more than 2 hours, but not more than 24 hours, and centrifuged at 3000 rpm for 5 minutes (Beckman Coulter Allegra 6R centrifuge). Sonicating animals before extraction reduces the normal extraction time from 24 hours to 2 hours (Båmstedt et al. 2000). Fluorescence was measured before and after acidification with 10% HCl with a TD-700 fluorometer. Concentrations of chlorophyll *a* and phaeopigment were calculated using the equations in Parsons et al. (1984) and Båmstedt et al. (2000).

For analysis of January 2013 and 2014 gut pigment samples we used a reduced extraction volume and minicuvette method to determine gut pigment from individual or small numbers of copepods (Takatsuji & Hamasaki 1997, Schnetzer & Steinberg 2002). Individuals, or groups of 2-3 copepods, of each species were homogenized in 1.0 mL of 90% acetone with extraction times similar to 2012 samples. Following extraction, samples were centrifuged at 3500 rpm for 5 minutes (Eppendorf 5424 centrifuge) and fluorescence was measured before and after acidification with a Turner Designs Trilogy with minicell insert. We analyzed 1-30 subsamples of copepods of the same species per time point.

2.3 Egestion rate

Egestion rates were determined for different copepod species by incubating copepods in whole (unfiltered) seawater and analyzing fecal pellet carbon produced through time (Urban-Rich et al. 1999, Wexels Riser et al. 2002). Fecal pellet carbon content was then used to calculate egestion rates for different species as follows:

$$E = [FPC / inds. / t] \times 24 \text{ hr.}$$

where E is egestion rate (µg C individual^{-1} day^{-1}), FPC is fecal pellet carbon (µg C), 'inds.' is number of copepods in the experiment, and t is incubation time (hr). Integrated egestion rates (µg C m^{-2} day^{-1}) for individual copepod species were estimated using measured abundances for each species over the entire 21-year PAL LTER time series (Chapter 2). We calculated integrated egestion rate for each species as the product of mean egestion rate (see above) and species integrated abundance (ind. m^{-2}) enumerated from 1x1m, 333 µm mesh net 0-300 m oblique tows collected in January 1993 – 2013 (n = 202). The integrated egestion rate for total copepods was calculated as the sum of individual species integrated egestion rates calculated (see above) for each tow enumerated. Results were used to assess contribution of different copepod species to carbon flux.

2.3.1 Fecal pellet production (FPP) experiments

Fecal pellet production (FPP) experiments were conducted at coastal process study sites (Figure 3.1, Appendix 2). Species used in each experiment was dependent on local abundance. In January, 2013 and 2014, we conducted 1-5 replicate experiments per species at each location, with a total of 16 experiments in 2013, and 29 in 2014.

For FPP experiments, cod end contents were gently transferred to a 60-L tub containing surface seawater at ambient temperature for sorting of copepods. Groups of copepods of each species were gently transferred to FPP chambers (fecatrons; Juul-Pedersen et al. 2006). Fecatrons were constructed from two nested 1L plastic containers, one with a 1 mm mesh bottom suspended inside the other container, and filled with water

collected below the chlorophyll maximum (to minimize the addition of large diatom chains that could not be separated from fecal pellets at the end of the experiment). The design allows pellets to fall through, preventing coprophagy or fragmentation of pellets by the copepods during the experiment (Urban-Rich et al. 1999; Wexels Riser et al. 2002, 2007). Wexels Riser et al. (2007) found a high proportion (92 %) of fecal pellets remained intact following incubations using this method. Each experiment comprised 1-5 replicate fecatrons, each containing the following number of individual copepods: *C. propinquus* (15-25), *C. acutus* (20-50), *R. gigas* (20-30), and *P. antarctica* (5-10). Copepods were incubated in fecatrons for 12-18 hours, remaining within ±1.0°C of ambient surface seawater temperature in flow-thru incubators kept in dim light conditions. We incubated 3 'control' fecatrons without copepods at each location.

Following incubations copepods were removed, counted, assessed if alive (any replicates with dead animals were discounted), transferred to cryovials, and immediately frozen at -80°C for later CN analysis. The contents of the 1-L fecatrons were filtered through a 64 μm sieve and transferred to an acid-washed petri dish for visual inspection. In some experiments copepods produced eggs which were removed. Fecal pellets were rinsed with 0.2 μm FSW onto combusted GF/F filters, stored in cryovials, and frozen at -80°C. Three replicate 0.2 μm FSW blanks were also analyzed using the same method, to account for carbon and nitrogen in the combusted GF/Fs and FSW. Three replicate initial and final water samples were collected in each experiment, filtered, stored at -80°C, and analyzed for chl *a* and phaeopigments on a Turner Designs Digital 10-AU fluorometer at Palmer Station immediately following each cruise (JGOFS Protocols, 1994).

Total organic carbon and nitrogen concentrations were determined using a method modified from Smith et al. (2000) to assess fecal pellet and animal elemental ratios. Pellets and animals were dried in an oven at 60°C for 72 hours, and total animal dry weight measured. Pellets (on combusted GFFs) and animals were transferred to combusted glassware (525°C for 2 hours), placed in a dessicator with a beaker containing ~20 mL of concentrated HCL for 12-14 hours to remove inorganic carbonates, and returned to the oven until completely dry. Subsamples of homogenized animal tissue (1-4 copepods) were weighed using a Sartorius XP1000P microbalance. The acidified, dried fecal pellet GF/Fs and animal subsamples were packed into tin capsules and processed using a Costech ECS 4010 CHNSO analyzer for flash combustion with acetanilide or atropine as the standard.

2.4 Daily Rations

Daily carbon rations, expressed as a percentage of body carbon ingested or egested per day, were calculated for each species from carbon content (mg C ind.$^{-1}$) and applied to daily carbon specific ingestion (*Section 2.2*) and egestion (*Section 2.3*) rates.

2.5 Data analysis

Regression analyses were used to test for significant correlations between integrated chl *a* and gut evacuation rate (k), ingestion rate (I), and egestion rate for each species. One-way ANOVAs were used to compare gut content (G), I, egestion rate, body dry weight and carbon content, and elemental ratios between different species.

One- and two-way ANOVAS were used to compare integrated chl *a*, k, G, and I values for *C. acutus, C. propinquus, and R. gigas* from experiments in 2012, 2013, and 2014 between four sub-regions: North-Coast, South-Coast, North-Slope, South-Slope. The shelf region was a transition between the coast and slope, thus we did not include it in our comparative analyses. These sub-regions encompass the variation in hydrographic and sea ice conditions in the WAP (Martinson et al. 2008, Stammerjohn et al. 2008). We also compared results of grazing and egestion experiments conducted at coastal stations in 2013 and 2014 with one- and two-way ANOVAS.

Data were rank transformed to meet normality and equal variance assumptions. Analyses were conducted using SigmaPlot 11.0. Only ANOVA results that were statistically significant ($p<0.05$) are described in results unless otherwise noted.

3. RESULTS

3.1 Physical environment, phytoplankton biomass and primary production

Sea surface temperature (SST) ranged from -1.8 to 2.8°C, and sea surface salinity (SSS) ranged from 32.1 to 33.8 at stations sampled in January 2012, 2013, and 2014. Integrated chl *a* ranged from 18.1 to 579 mg m^{-2}, and integrated primary production (PP) ranged from 368 to 5430 mg C m^{-2} day^{-1}. (See also Appendix 1 and 2) Note that SSS and PP do not include values for 2014 as data were not available.

3.2 Copepod grazing

3.2.1 Gut evacuation rate constant (k)

Hourly gut evacuation rate constants (k) were lowest on average for *Calanoides acutus* (0.373 h^{-1}), about half the average for *Calanus propinquus* (0.606 h^{-1}) and *Rhincalanus gigas* (0.634 h^{-1}; Table 3.1). This equaled gut passage times (1/k) ranging from 1.2 - 9.5 hours for *C. acutus* and 0.4 - 5 hours for *C. propinquus*, gut passage time for *R. gigas* was under 4 hours for all experiments.

The positive linear relationships between water column chl *a* and k for *C. acutus* and *C. propinquus* were significant (Figure 3.2). We therefore used this relationship to estimate the k value applied in ingestion rate calculations (see *Section 3.2.2*) at stations where GER experiments were not conducted. *R. gigas* gut evacuation rates did not trend with chl *a* (Figure 3.2), so we used the *R. gigas* average gut evacuation rate of 0.634 h^{-1}

in ingestion rate calculations. Since we did not conduct GER experiments with *Metridia gerlachei,* we applied an average gut evacuation rate from the literature of 1.0 h^{-1} (Froneman et al. 2000, Li et al. 2001, Pakhomov and Froneman 2004).

3.2.2 Individual gut content (G) and ingestion rates (I)

The average initial gut contents for *R. gigas* and *C. propinquus* were 2-10 times higher, and ingestion rates over three times higher, than those of *C. acutus* and *M. gerlachei*, which had ingestion rates up to 0.8 and 1.4 µg {Chl *a* equiv.} $ind.^{-1}$ day^{-1}, respectively (Table 3.2). *C. acutus* and *R. gigas* had lower gut contents at higher chl *a* concentrations (>400 mg m^{-2}) (Figure 3.3). We were unable to sample *C. propinquus* at stations with higher chl *a*.

Ingestion rate of *C. acutus*, *C. propinquus*, and *R. gigas* increased with increasing chl *a* concentration (Figure 3.4). We used these significant positive linear relationships, and the average ingestion rate of *M. gerlachei* (24.0 ng {Chl *a* equiv.} $ind.^{-1}$ day^{-1}) (Table 3.2) to determine the ingestion rate use in integrated grazing rate calculations (see *Section 3.2.3*). For Clausocalanidae and *Oithona* sp., we applied an ingestion rate from the lower end of the literature of 38 and 16 ng {Chl *a* equiv.} $ind.^{-1}$ day^{-1}, respectively (Atkinson 1996; Bernard and Froneman 2005, 2003; Pakhomov and Froneman 2004).

3.2.3 Integrated grazing rates and grazing impact

The six copepod species used in our total copepod integrated grazing calculations represent an average of 95% (77 - 100%) of the abundance of non-carnivorous WAP copepods (Oresland 1991, Yen 1991; Chapter 2). Of the six species, *M. gerlachei* had

the highest average integrated grazing rate (15.1 µg {Chl *a* equiv.} m^{-2} day^{-1}) and contributed to an average of 43% of the total copepod grazing over the 21-year PAL LTER times series (Table 3.3). While the average integrated grazing rate for *C. acutus* (14.3 µg {Chl *a* equiv.} m^{-2} day^{-1}) was similar to *M. gerlachei*, this value is influenced by one station (-100.000 in 2011) with a record abundance of *C. acutus* (44,378 ind. m^{-2}), yielding a grazing rate of 1459 µg {Chl *a* equiv.} m^{-2} day^{-1} (Table 3.3). Excluding this outlier, the average integrated grazing rate for *C. acutus* was 6.72 µg {Chl *a* equiv.} m^{-2} day^{-1}. Even including the outlier tow *C. acutus* only contributed to an average 8% of copepod grazing, behind *Clausocalanus* sp. (23%), *Oithona* sp. (14%), and *R. gigas* (9%). *C. propinquus* had the lowest contribution to total copepod grazing of 3% (Table 3.3).

The combined daily grazing impact of the six copepod species was low, removing < 1% of both phytoplankton biomass and primary production daily, on average (Table 3.3). Grazing impact ranged from 0.1 -1% of phytoplankton biomass and <1 -11% of primary production.

3.2.4 Regional comparison

Water-column integrated chl *a* was an order of magnitude higher along the coast than the slope ($p = 0.023$), but there was no significant difference between north and south within either the coast or slope (Figure 3.5a). Differences between sub-regions for gut evacuation rate (k), initial gut content (G), and daily ingestion rate for *C. acutus, C. propinquus,* and *R. gigas* (Figure 3.5b-d) generally follow the trends in chl *a*, with some exceptions. Gut evacuation rates do not vary greatly among locations for each species;

the only significant regional difference is between the North-Coast and South-Slope for all species combined ($p < 0.05$). While *R. gigas* has little regional variation in gut evacuation rate, their gut content and ingestion rates were 30-70 times higher (significantly) on the coast than the slope (for both north and south) (Figure 3.5b-d) and no significant latitudinal differences were found. *C. acutus* and *C. propinquus* gut contents and ingestion rates were also significantly greater on the coast than the slope (for both north and south), but only 10-40 and 4-10 times greater for *C. acutus* and *C. propinquus*, respectively (Figure 3.5c). Both species had significantly greater ingestion rates on the North-Coast than South-Coast. *C. acutus* had the same trend for gut contents, while *C. propinquus* had more gut contents (although not significantly) on the South-Coast (Figure 3.5c,d). Significant differences in gut contents and ingestion rates between species existed in each region for the North-Coast and South-Coast, but not on the slopes.

3.3 Copepod egestion

Egestion rates ranged from 0.82 – 37.3 µg C ind.$^{-1}$ day^{-1}, with average species egestion rates of 3.66 µg C ind.$^{-1}$ day^{-1} (*C. acutus*), 6.98 µg C ind.$^{-1}$ day^{-1} (*C. propinquus*), 2.95 µg C ind.$^{-1}$ day^{-1} (*R. gigas*), and 15.4 µg C ind.$^{-1}$ day^{-1} (*Paraeuchaeta antarctica*) (Table 3.4). *C. propinquus* had the highest egestion rate of the herbivorous and omnivorous copepods, significantly higher than *R. gigas* ($p = 0.007$), the copepod with the lowest egestion rate. While *C. acutus* egestion increased with increasing chl *a* ($r^2 = 0.30$) and SST ($r^2 = 0.46$), this increase was not statistically significant for this or any other species. We therefore used the average egestion rate for each species (*P. antarctica* = 15.4, *C. propqinquus* = 7.0, *C. acutus* = 3.7, *R. gigas* = 2.9 µg C ind.$^{-1}$ day^{-1}) to

calculate integrated egestion rates. Fecal pellet C:N elemental ratios ranged from 1.7 – 28.5, but the mean was similar (~7) for all species (Table 3.4).

C. acutus has the highest integrated egestion rate, with average fecal pellet production of 2.3 mg C m^{-2} day^{-1} over the 21-year time series, and up to 162 mg C m^{-2} day^{-1} at one station with high *C. acutus* abundance (Table 3.5). Even without this outlier station included, the average *C. acutus* integrated egestion rate is an order of magnitude higher than all other species. *P. antartica* has the lowest integrated egestion rates, despite having the highest individual egestion rate. *P. antarctica* is calculated for adult copepods only.

Chl *a* was not completely depleted in any experiments, thus animals were not starved during the incubation. The exception was the carnivorous copepod *P. antarctica* as we did not feed them additional prey. But, even with no added prey, *P. antarctica* produced the highest egestion rates (up to 37 µg C $ind.^{-1}$ day^{-1}), significantly greater than *R. gigas* ($p = 0.003$) and *C. acutus* ($p = 0.007$), and twice that of *C. propinquus* (Table 3.4).

3.4 Copepod daily rations

Copepod dry weight and carbon content differed among species ($p<0.001$); *P. antarctica* was the largest copepod with both dry weight (4.4 mg) and carbon content (3.1 mg C) on average 3-5 times greater than the other copepod species (0.8 – 1.5 mg dry wt. and 0.4 – 0.7 mg C) (Table 3.6). *P. antarctica* and *C. acutus* had a significantly higher C:N ratios (7.7 and 7.3, respectively) on average than *C. propinquus* (5.1) and *R. gigas* (4.7). Furthermore, *R. gigas* had the lowest carbon content (~33%), significantly lower

than all other copepod species examined (44-48%; Table 3.6). We used mean carbon content (mg C) for each species to calculate body rations.

The proportion of body carbon ingested daily as phytoplankton was low for *C. acutus, C. propinquus* and *R. gigas* and ~1% (Table 3.6). Among these three species, *C. propinquus* and *R. gigas* had slightly higher daily rations, consuming up to 13% of their body carbon per day as phytoplankton. The proportion of body carbon egested daily was also low: ~1% for all species, with *C. propinquus* (the copepod with highest body C) egesting a slightly higher proportion (up to 3.6%; Table 3.6). We did not use these data to determine egestion:ingestion ratios since GER and FPP experiments were not always conducted with animals from the same location.

3.5 Ingestion and egestion during a large phytoplankton bloom

We compared copepod ingestion and egestion experiments conducted on the coast in 2013 post-bloom and 2014 during peak bloom conditions in the WAP, as determined by time-series sampling of chl *a* from November - March at Palmer Station on the coast (Figure 3.1). Stations sampled in January 2014 had extremely high chl *a* in the coastal regions of the WAP due to late seasonal ice retreat, and a delayed spring bloom occurring in January (compared to November/December in 2013; O. Schofield, pers. comm.). Average (± SD) integrated chl *a* for coastal stations sampled in 2014 was 335 ± 152 mg m^{-2} (n = 10), with surface chl *a* as high as 23 mg m^{-3}. In the austral summer of 2012/2013 sea ice retreat occurred 44 days earlier (S. Stammerjohn, pers. comm.), with peak bloom (surface chl *a* = 30 mg m^{-3} near Palmer Station; O. Schofield, pers. comm.) in late

November; by January 2013 coastal chl *a* was significantly lower ($p = 0.005$): 92.9 ± 51.3 mg m^{-2}.

During higher phytoplankton biomass conditions in January 2014, *C. acutus* and *C. propinquus* gut evacuation rates were, on average, twice as fast (higher k) as in 2013 (statistically significant for *C. propinquus*, $p = 0.002$), whereas initial gut contents for both species was similar in 2013 and 2014 (Figure 3.6a,b). The resulting ingestion rates were significantly greater for both species in 2014 ($p = 0.032$ for *C. acutus*, $p < 0.001$ for *C. propinquus*) (Figure 3.6c). However, gut evacuation rates were similar in both years for *R. gigas*, but gut content over six times greater ($p < 0.001$) in 2014, resulting in ingestion rates over an order of magnitude greater in 2014 (Figure 3.6a-c).

The daily body rations (% body C ingested day^{-1}) for *C. acutus* and *R. gigas* were also significantly higher in 2014, with *C. acutus* increasing from 0.3% to 1.2% (from 2013 to 2014, respectively), and *R. gigas* increasing from 0.3% to 3.3%. *C. propinquus* daily body ration increased from 1.6% to 2.5%, but the difference was not significant. Daily egestion rates, fecal pellet C:N ratio, and egestion body ration were not significantly different between years.

4. DISCUSSION

4.1 Species-specific grazing rates

4.1.1 Gut evacuation rates

Gut evacuation rates (k) for copepods and other mesozooplankton are highly variable as they can depend upon temperature, phytoplankton biomass and quality, as well as zooplankton vertical migration, diel periodicity, and feeding strategy (Dagg & Walser Jr. 1987; Dam & Peterson 1988; Atkinson et al. 1992, 1996a; Atkinson 1996; Schnetzer & Steinberg 2002). The range in phytoplankton biomass (18 – 579 mg Chl *a* m^{-2}) and temperature (-1.5 to 2.1°C) in our study is the widest among Southern Ocean copepod grazing studies south of the Antarctic Polar Front (APF) (Table 3.7). Thus it is not surprising that we found a wide range in k (h^{-1}) for each copepod species (*Calanus propinquus*, 0.2 – 2.5; *Rhincalanus gigas* 0.3 – 2.0; *Calanoides acutus*, 0.1 – 0.8). Gut evacuation rates for *C. propinquus* spanned the range reported in literature, those for *R. gigas* were at the low end, and most k values for *C. acutus* fell below literature values (Table 3.7). This is likely because previous studies of *C. propinquus* occurred in regions where SST was 0°C or below, while previous studies of *R. gigas* and *C. acutus* include warmer regions near the APF (sub-Antarctic). Since k trends positively with temperature (Dam & Peterson 1988), due to higher metabolic rate in warmer regions, a lower k for *R. gigas* and *C. acutus* is expected for our higher latitude, colder study region. Gut

evacuation rates for all three copepods (mean= 0.6, range = 0.1 – 2.5) were on average higher than rates found in the WAP for the pteropod *Limacina helicina* (k = 0.3 h^{-1}), and the upper range of k for copepods was higher than that for Antarctic krill, *Euphausia superba* (k = 1.0 – 1.9 h^{-1}) (Bernard et al. 2012). This is expected, as copepods are smaller animals with shorter gut passage times.

We also found a significant positive linear relationship between k and chl *a* for the species *C. acutus* and *C. propinquus*. A similar trend has been reported at higher latitudes (Dagg & Walser Jr. 1987, Atkinson et al. 1996b), with lower gut evacuation rate at low chlorophyll levels, while in temperate regions (with higher variation in temperature) k trends positively with SST (Dam and Peterson 1988) as long as food is not limiting.

4.1.2 Individual gut content

Average gut contents for *R. gigas C. propinquus,* and *C. acutus* (10.7, 8.4, and 4.3 ng {Chl *a* equiv.} $ind.^{-1}$, respectively) were at the high end of literature values for the Southern Ocean (Atkinson et al. 1992, 1996a; Dubischar & Bathmann 1997; Tirelli & Mayzaud 1999; Li et al. 2001; Pakhomov & Froneman 2004b), with maximum values (e.g., over 30 ng {Chl *a* equiv.} $ind.^{-1}$) as high as those reported by Atkinson et al. (1996a) (e.g., 10-120 ng {Chl *a* equiv.} $ind.^{-1}$) during a phytoplankton bloom with surface chl *a* ranging from 6.5 – 19 mg m^{-3}. One explanation for the high gut chl *a* content and low gut evacuation rates of copepods in our study is that copepod feeding can reach saturation or decrease at high chl *a* concentrations (Atkinson et al. 1996a). At stations with the highest chl *a* (>400 mg m^{-2} and surface chl *a* up to 23 mg m^{-3}), *C. acutus*

and *R. gigas* gut contents averaged 64% (as low as 8%) and 84% (as low as 54%), respectively, of gut contents at stations where chl *a* was lower (155 - 382 mg m^{-2} and surface chl *a* 1 – 14 mg m^{-3}) (Figure 3.3). Similarly, Atkinson et al. (1996a) found little difference in gut contents of *C. acutus*, *R. gigas,* and *C. propinquus* during a bloom (mentioned above) compared with those collected during a moderate bloom (integrated chl *a* 223 mg m^{-2} and surface chl *a* 1 – 4 mg m^{-3}; Atkinson et al. 1992), suggesting saturation. In addition, gut evacuation rates in a bloom were one half to one third of those recorded at lower food concentrations (Schnack-Schiel et al. 1985, Atkinson 1995).

A second explanation for some of the high gut pigment contents found in our study is the increased sensitivity gained from fluorescence analysis of individual copepods using reduced extraction volume and minicuvette methods. No other study of Southern Ocean copepods has used this method, instead analyzing groups of individuals (~5-50), which can mask individual difference in gut pigment contents (Takatsuji & Hamasaki 1997, Schnetzer & Steinberg 2002). While we usually conducted tows during daylight hours, we recognize the possibility of diel variability in feeding, as many studies report highest gut content at night (Atkinson et al. 1992, Li et al. 2001, Bernard & Froneman 2003) although this effect is reduced at high latitudes due to reduced hours of darkness (Conover & Huntley 1991).

4.1.3 Daily ingestion rates and rations

Average daily ingestion rates for *C. acutus, C. propinquus, R. gigas*, and *Metridia gerlachei* were within those reported in literature (Table 3.7), with maximum rates for all (except *M. gerlachei*) among the highest previously reported for Southern Ocean

copepods (Atkinson et al. 1992, Atkinson et al. 1996a). This is expected since ingestion rate is calculated as the product of k, which in our study was below previous literature values, and initial gut content, which was above previous literature values. We were only able to collect *M. gerlachei* at a few stations, but our results are consistent with ingestion rates for *M. gerlachei* lower than for *C. acutus* (Table 3.7; Li et al. 2001, Pakhomov and Froneman 2004a).

C. propinquus and *R. gigas* ingestion rates were 4-5 times higher on average than *C. acutus* and *M. gerlachei*, which is not surprising as the former are larger copepods with higher gut pigment contents. Individual ingestion rates for *C. propinquus* and *R. gigas* (mean = 133 ng {Chl *a* equiv.} ind.$^{-1}$ day^{-1} for both species) were higher than those reported in the WAP for the abundant small euphausiid *Thysanoessa macrura* (10 – 120 ng {Chl *a* equiv.} ind.$^{-1}$ day^{-1}), and lower then those reported for the pteropod *Limacina helicina*, and euphausiids *Euphausia crystallorophias*, and juvenile *E. superba* (920 – 6620 ng {Chl *a* equiv.} ind.$^{-1}$ day^{-1}; Bernard et al. 2012), although a few *C. propinquus* with maximum ingestion rates (~1400 ng {Chl *a* equiv.} ind.$^{-1}$ day^{-1}) were at the low end of their range. Ingestion rates for large adult *E. superba* (up to 8950 ng {Chl *a* equiv.} ind.$^{-1}$ day^{-1}) were an order of magnitude higher than those of copepods in our study (Bernard et al. 2012).

Despite the high copepod gut pigment/C content and ingestion rates relative to larger animals, phytoplankton contribution to the diet of the copepods was low (mean daily rations of 0.6% for *C. acutus*, 1.3% for *C. propinquus*, and 2.0% for *R. gigas*). Copepod daily rations in our study were within range of most previous summer studies (Table 3.8), with the exception of *R. gigas,* which was higher in our study. Schnack

(1985) reported daily rations up to 10% for *R. gigas* and > 20% for *C. acutus* and *C. propinquus* in the Antarctic Peninsula, but few studies have reported rations that high (Atkinson et al. 1992). Although copepods could meet their metabolic requirements (3.4-3.8% for respiration and an additional 1.6-4.5% for egg production; Dagg et al. 1982, Schnack-Schiel et al. 1991, Conover & Huntley 1991, Atkinson et al. 2012b) feeding on phytoplankton alone, average daily rations are below those needed to satisfy metabolic costs, and would not fuel reproduction (Huntley et al. 1991, Conover & Huntley 1991). This is not an uncommon result for Southern Ocean copepods (Atkinson & Shreeve 1995, Mayzaud et al. 2002, Calbet et al. 2006, Lee et al. 2013), and indicates additional food sources, such as protozoans and metazoans. Omnivorous feeding is common among copepods. For example, *C. propinquus* is a known omnivore, even during spring and summer blooms when phytoplankton is abundant (Schnack-Schiel et al. 1991; Hopkins et al. 1993; Bathmann et al. 1993; Atkinson 1995, 1998; Atkinson et al. 1996a). *R. gigas* and *C. acutus* were previously considered mostly herbivorous during the austral spring and summer, feeding indiscriminately on phytoplankton (Atkinson & Shreeve 1995; Atkinson 1995, 1998; Atkinson et al. 1996a). Yet more recently in a northern WAP study, Calbet et al. (2006) suggest these copepods feed more selectively based on size, motility and quality of prey, with *C. acutus*, *R. gigas* and *C. propinquus* having high clearance rates and preference for motile cells (e.g., ciliates and *Gyrodinium* spp.), although the highest carbon intake was from autotrophs.

Low carbon intake from phytoplankton is also evident for other mesozooplankton in the WAP during summer. Bernard et al. (2012) examined daily rations of euphausiids using the same methods, and also found a low contribution of phytoplankton in their diet

(daily rations on average 0.3% with a maximum of 3% for *E. superba*), suggesting protozoans are also an important component of their diet. Furthermore, larger salps (*Salpa thompsoni*) and *L. helicina* daily rations (15% and 1-27%, respectively) also indicate consumption of other sources of carbon at times (Bernard et al. 2012). Predation of copepods and other zooplankton on protozoans or other metazoans in the WAP needs to be directly examined.

4.1.4. Regional comparison

Phytoplankton biomass and composition in the WAP varies both along a coast-shelf-slope gradient (Vernet et al. 2008), and a latitudinal gradient (Montes-Hugo et al. 2008). We found highest chl *a* near the coast (mean 245 mg m^{-2}), 93 mg m^{-2} average over the shelf, to 20 mg m^{-2} in the slope region. Phytoplankton in the WAP in summer is mostly dominated by large (>20μm) diatoms, but due to warming, regional differences have been developing over the last two decades with a shift toward smaller cells north of our study region (Montes-Hugo et al. 2008, 2009; Vernet et al. 2008). Considering these gradients, we examined regional variation in copepod grazing to elucidate how the changes associated with the climate gradient in the WAP might impact copepod grazing.

Copepod grazing generally corresponded with regional differences in chl *a*, with higher gut content and ingestion rates on the coast than slope; the shelf appears to be a transition between the two. This is consistent with previous studies comparing phytoplankton blooms to oceanic conditions, with similar differences in phytoplankton biomass (Atkinson et al. 1992, 1996a; Li et al. 2001). Gut evacuation rate varied less with chl *a*, which further suggests saturation of feeding at higher chl *a* concentrations in the

coastal regions (Atkinson et al. 1996a). However, we conducted fewer GER experiments on the slope than coast, so our k values are not as well constrained for the slope.

Since daily rations are calculated from the ingestion rate applied to body carbon content, relative regional differences in ration for each species reflect that of ingestion rate. *C. propinquus* and *R. gigas* had significantly higher average rations on the coast (2.0% and 2.6%, respectively) than slope (0.2% and <0.1%), suggesting they are primarily herbivorous on the coast and more carnivorous on the slope (Atkinson & Shreeve 1995, Calbet et al. 2006, Lee et al. 2013). Bernard et al. (2012) showed similar regional differences in *E. superba* diet between the coast and slope. Thus, if a shift towards decreased phytoplankton biomass and smaller phytoplankton continues farther south in the WAP (Montes-Hugo et al. 2009), copepods and other zooplankton will need to supplement their diet with microzooplankton (Garzio & Steinberg 2013) or smaller phytoplankton.

The only significant difference with latitude was for *C. acutus* gut content and ingestion rate in the coastal regions. There *C. acutus* followed the trend in chl *a* most strongly, indicating a close correlation to phytoplankton biomass. *C. acutus* body ration was also significantly higher in the North, Coast (1.5%), than South, Coast (0.5%). These daily rations are lower than *C. propinquus* and *R. gigas* along the coast, but could be enough to support metabolic needs as *C. acutus* can use their excess lipid stores for winter diapause well into the next season (Calbet et al. 2006). Daily rations on the slope for *C. acutus* (<0.3%) are well below metabolic requirements, similar to those of *C. propinquus* and *R. gigas*. While *C. acutus* can quickly clear large motile cells (i.e. ciliates and dinoflagellates), they are primarily herbivores with a preference for large diatoms

important in building their lipid stores (Atkinson 1998, Calbet et al. 2006, Pasternak et al. 2009). Thus the predicted shift to smaller phytoplankton in the WAP could remove a critical source of nutrition for *C. acutus*.

4.2. Total copepod integrated grazing rates and grazing impact

The mean total copepod daily integrated grazing rate (3.1 mg C m^{-2} day^{-1}) was within the range found previously in the Southern Ocean in spring and summer (<0.1 - 94 mg C m^{-2} day^{-1}; Schnack-Schiel et al. 1985; Atkinson 1996; Razouls et al. 1998; Cabal & Alvarez-Marqués 2002; Mayzaud et al. 2002; Bernard & Froneman 2003, 2005; Tanimura et al. 2008), although we saw that high abundance of one species (for example *C. acutus* in 2011) can result in grazing rates up to 92 mg C m^{-2} day^{-1}. We note that total copepod integrated grazing rate as calculated (applying ingestion rates in this 3-yr. study to species abundances 1993-2013) is subject to error resulting from inter-annual differences in environmental conditions (e.g., temperature, phytoplankton biomass). For example, ingestion rates for *C. acutus, C. propinquus,* and *R. gigas* were applied to net abundance based on a linear relationship with chl *a*; if these copepods become food saturated, this relationship would overestimate grazing rate at high chl *a* concentrations. Conversely, total copepod integrated grazing rate could be underestimated as it does not include *Oncaea* sp. and earlier stage copepodites, which have been reported to be important contributors to copepod grazing (Schnack-Schiel et al. 1985, Atkinson et al. 1996a, Bernard & Froneman 2005).

The WAP copepods had low impact on phytoplankton standing stock (<0.1 – 1%) and primary production (<1 - 11%). This is comparable to previous studies of the same

copepod species grazing impact ranging from <1 – 4% of chl *a* and <1 – 55% of primary production (Schnack-Schiel et al. 1985, Atkinson & Shreeve 1995, Atkinson 1995, Atkinson et al. 1996a, Razouls et al. 1998, Cabal & Alvarez-Marqués 2002, Tanimura et al. 2008, Lee et al. 2013). Combined grazing of euphausiids, pteropods, and salps in the WAP in summer (excluding regions with salp blooms where grazing impact is up to 30% phytoplankton standing stock) was <0.3% of phytoplankton standing stock and <0.6% of productivity (Bernard et al. 2012). Combining the results with those of Bernard et al. (2012), we estimate mean meso- plus macrozooplankton community grazing impact of ~0.5% phytoplankton standing stock and ~1.2% of primary production. This is relatively low compared to summer microzooplankton grazing in the WAP, which was on average 55-85% of primary production (Garzio et al. 2013). Although microzooplankton are the most important grazers of phytoplankton in the WAP, krill swarms, salp blooms, or copepod aggregations would result in higher localized mesozooplankton grazing contribution.

4.3. Copepod egestion

Herbivorous copepods (*C. acutus, R. gigas*, and *C. propinquus*) had an average (± SD) daily egestion rate of 5.5 ± 1.7 μg C ind^{-1} day^{-1}, on the higher end of previously reported copepod egestion rates at high latitudes (Table 3.9). This is not surprising since the WAP is a productive continental shelf with a high contribution of zooplankton fecal pellets to POC export, especially in summer (67%, up to 100%; Gleiber et al. 2012), compared to other high-latitude regions (Wassmann et al. 1999, Dagg et al. 2003, Wexels Riser et al. 2008, Smith et al. 2011). Indeed copepods were the second highest

contributors to zooplankton fecal pellet flux (22%) after krill (72%) as measured by a moored sediment trap suspended at 170 m in the northern WAP (Gleiber et al. 2012). To our knowledge, this is the first study reporting egestion rates for *Paraeuchaeta antarctica*.

Daily individual egestion rates differed significantly among copepod species, with *R. gigas* and *C. acutus* having the lowest average rates (3 and 3.7 μg C ind^{-1} day^{-1}, respectively) and *C. propiquus* and *P. antarctica* higher average rates (7 and 15.4 μg C ind^{-1} day^{-1}). Few previous studies in the Southern Ocean conducted incubations for copepod fecal pellet production (Dubischar & Bathmann 2002, Dagg et al. 2003), and of these only Dagg et al. (2003) reported species-specific copepod egestion rates. Their findings (reported in hourly fecal pellet production) corresponded to egestion rates of up to 1.65 μg C ind^{-1} day^{-1} for *R. gigas*, 2.24 μg C ind^{-1} day^{-1} for *C. propinquus*, and 3.6 μg C ind^{-1} day^{-1} for *C. acutus*. In comparison, egestion rates found in the present study were up to 10 times higher. This discrepancy could be due to a higher phytoplankton biomass at some stations in our study, but this explanation is unlikely because stations with comparable concentrations of chl *a* to Dagg et al. (2003) still had higher egestion rates. Another explanation is the high variability of zooplankton fecal pellet production and differences in the environment: Dagg et al. (2003) sampled near the Antarctic Polar Front with smaller cells (Urban-Rich et al. 2001), and the present study is at relatively higher latitudes with large diatoms dominating the phytoplankton community. We note that our egestion rates could also be overestimated, as it was difficult to entirely remove large diatom chains and eggs from fecal pellets collected in fecatrons at the conclusion of FPP experiment.

Fecal pellet C:N elemental ratios ranged from 3.9 – 22.2, with average pellet C:N ratios of 7-8, similar to that reported for copepod fecal pellets at high latitudes (Morales 1987, Urban-Rich et al. 1999). Fecal pellet C:N ratios were on average slightly higher than copepod body elemental ratios (4.7 – 7.7); this is consistent with reports of copepods fecal pellets and other zooplankton bring N-depleted since zooplankton assimilate nitrogen more efficiently than carbon (Morales 1987, Mayor et al. 2011, Atkinson et al. 2012a)

Average total copepod integrated egestion rate (~2.5 mg C $m^{-2}day^{-1}$) was lower than in most previous studies at high latitudes (Table 3.9); although maximum rates associated with high densities of copepods ranged on the higher end of literature values. We note that total copepod integrated egestion rate calculated in this study is an underestimate as we only included four species, excluding about 75% of other copepods by number (Chapter 2). However, many of the abundant copepods are small (e.g., *Oithona* sp., Clausocalanidae, *Oncaea* sp.; Chapter 2), and would produce smaller, slower sinking fecal pellets that are attenuated more rapidly in the water column than larger pellets (Dagg et al. 2003, Steinberg et al. 2008) from microbial degradation, horizontal transport, destruction from turbulence, and zooplankton fragmentation or ingestion (González & Smetacek 1994, Dagg et al. 2003, Wexels Riser et al. 2007, Sampei et al. 2008). Møller et al. (2011) calculated fecal pellet retention in the water column from *in situ* fecal pellet flux and fecal pellet production. Using the average total copepod integrated egestion rate from our study (~1.4 mg C $m^{-2}day^{-1}$; adjusted to 170m) and average copepod fecal pellet flux at 170 m from a sediment trap (0.61 mg C $m^{-2}day^{-1}$; Gleiber et al. 2012), we estimate 58% retention of fecal pellets from large copepods in

the upper 170 m of the water column. This compares to >80% retention of copepod fecal pellets in the Southern Indian Ocean north of the Antarctic Polar Front (Møller et al. 2011) and 37-96% retention in the Barents Sea (Wexels Riser et al. 2002, 2007). This potential high retention of copepod fecal pellets indicates they may not be efficient for carbon export in the WAP, at least compared to krill fecal pellets (Gleiber et al. 2012).

4.5. Copepod grazing and egestion during a large phytoplankton bloom

Sea ice extent was a record high during the 2013-14 sea ice season in the WAP (19.57×10^6 km^2 for the entire Southern Hemisphere) with the latest sea ice retreat (Julian day 366, recorded near Anvers Island) since 1984-85. The prior season (2012-13) day of sea ice retreat was also later than average, but occurred about 44 days earlier compared to 2013-2014 (S. Stammerjohn, pers. comm.). Therefore, sampling in January 2014 coincided with the peak of the spring phytoplankton bloom, with high surface chl *a* concentrations over 20 μg L^{-1}, while January 2013 sampling was during the decline of the spring bloom (maximum surface chl *a* = 10 μg L^{-1}). This interannual variability between the two seasons allows comparisons between copepod grazing and egestion during the spring bloom and post-bloom.

The three copepod species represent a range of feeding and life history strategies. *C. acutus* is a true polar species that undergoes diapause in the winter and feeds primarily on phytoplankton during the spring bloom, while *C. propinquus* feeds throughout the winter (on protozoans and small copepods; Atkinson 1998, 1991; Pasternak and Schnack-Schiel, 2001a; Schnack-Schiel, 2001). *R. gigas* falls between these two strategies, often (but not always) going through diapause and feeding preferentially on phytoplankton, but

also on detritus, protozoans, and metazoans (Ward et al. 1997, Atkinson 1998). All three species, however, shift their feeding strategies depending on food availability (Atkinson 1998, Calbet et al. 2006, Pasternak et al. 2009). During the spring bloom these copepods would be expected to be almost entirely herbivorous. Comparing the two years, copepods had higher ($p < 0.001$) percent body carbon content during the peak bloom in 2014, which is predicted for copepods feeding primarily on phytoplankton (Atkinson & Shreeve 1995, Lee et al. 2013). The higher daily body carbon rations for all three species in 2014 (on average 1.2 – 3.3%) compared to 2013 (0.3 – 1.6%) suggests a shift in diet, from phytoplankton during the bloom to other sources of carbon (i.e., protozoans or metazoans) post-bloom. This corresponds to ingestion rates that were more than double for all three species in 2014. *R. gigas* daily ration increased almost an order of magnitude from 2013 to 2014 (0.4 to 3.3%). Despite this increase in ingestion rate, gut evacuation rate was almost the same for *R. gigas* during bloom and post-bloom conditions, while gut evacuation rates were twice as fast for *C. acutus* and *C. propinquus* during the bloom. We posit that *R. gigas* may have reached feeding saturation more quickly in higher chl *a* conditions than the other species (Atkinson et al. 1992, 1996a). *C. propinquus* grazing changed little between years, suggesting their reliance on phytoplankton only slightly increases in high biomass and they still gain much of their nutrition though omnivory (Urban-Rich et al. 2001).

While copepod grazing increased in 2014, egestion rates and fecal pellet C:N ratios remained similar to those in 2013. Increased egestion generally coincides with increased feeding rates (Dagg & Walser Jr. 1987, Atkinson et al. 2012a), but similar

egestion at higher food concentrations could indicate that copepods are feeding while saturated (Dagg et al. 2003).

5. SUMMARY AND CONCLUSIONS

Copepods are a key component in the Southern Ocean food web as grazers of phytoplankton, as well as a link to the microbial loop via feeding on microzooplankton and detritus (Atkinson 1995, 1998; Pasternak & Schnack-Schiel 2001b; Calbet et al. 2006). Our study builds on prior Southern Ocean copepod grazing studies, with results that span a wide range of temperatures and chl *a* conditions, and is the first to examine copepod grazing in the southern WAP. Copepod gut evacuation rates were lower, and gut content and ingestion rates generally higher, than those reported in previous studies near the APF. Gut content and ingestion rates from stations with the highest phytoplankton biomass (>400 mg m^{-2}) were lower than at stations with moderate chl *a,* indicating that copepods reach saturation when feeding in high phytoplankton conditions, an hypothesis that is consistent with prior studies comparing copepod grazing in high biomass conditions (Atkinson et al. 1992, 1996).

The larger copepods *Calanus propinquus* and *Rhincalanus gigas* had 2-4 times greater gut evacuation rates, initial gut contents, and ingestion rates than *Calanoides acutus*. However, smaller, numerically dominant species (*Metridia gerlachei*, Clausocalanidae, and *Oithona* spp.) likely have a higher contribution to grazing, and *C. acutus* can also be an important contributor to biomass. Total copepod community impact on removal of phytoplankton standing stock and production was low (<1% on average), although impact on primary production could range up to 11% in regions with large

copepod aggregations. This confirms results indicating that microzooplankton, as opposed to meso- and macrozooplankton (e.g., copepods, krill, salps, pteropods), are the dominant grazers of phytoplankton in the WAP (Bernard et al. 2012, Garzio et al. 2013). However, future studies on the grazing of smaller copepod species and copepodite stages of larger species are needed.

Our comparison of copepod grazing and body rations between regions and years with different chl *a* concentrations suggest a shift in feeding mode from mostly phytoplankton in high-bloom conditions on the coast, to increased reliance on other sources of carbon (i.e., metazoans and protozoans) in lower chl *a* conditions and offshore. Climate change in the WAP has manifested in phytoplankton with decreasing chl *a* concentrations north of the study region, predicted to continue south-ward with increased warming due to lower sea ice and increased winds (Stammerjohn et al. 2008, Montes-Hugo et al. 2009). Our results suggest that copepods near the WAP could survive in lower chlorophyll concentrations by supplementing their diet with microzooplankton and protozoans. However, further studies are needed to understand the impact of increased top-down pressure by copepods on lower trophic levels, and survival of copepods in prolonged conditions of low phytoplankton biomass. We also found high egestion rates, even in low chl *a* conditions, but with relatively high retention of fecal pellets in the upper water column. Thus, compared to krill, copepods may not be efficient exporters of C to depth in this region.

Effects of warming in the WAP are impacting the entire pelagic marine ecosystem, from plankton to top predators (Ducklow et al. 2012, Steinberg et al. 2012b). Long-term trends in copepod abundance from 1993-2013 indicate they are increasing in

the WAP due to decreasing sea ice, with an earlier retreat, and increasing phytoplankton biomass and productivity (Chapter 2), and there are long-term changes in the dominant macrozooplankton as well (Steinberg et al. in review). Therefore understanding the role of copepods in energy transfer through the food web and export in the WAP further elucidate the mechanisms leading to interannual variability of summer copepod abundance, and can be used to predict how the copepod community will respond to future environmental changes.

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Table 3.1. Gut evacuation rates and passage times for copepods *Calanoides acutus*, *Calanus propinquus*, and *Rhincalanus gigas*. r^2 and p-values are given for exponential curve fit. Mean and standard deviations are listed for gut evacuation rates and passage times for each species. Chl *a* is integrated to 100 m. 'Grid station' is the PAL LTER station identification (Waters and Smith, 1992), see Appendix 1 for latitude and longitude coordinates. All experiments were performed in January in the listed year.

Copepod species	Gut evacuation rate (k, h^{-1})	r^2	p	Gut passage time (1/k, h)	SST (°C)	Chl *a* (mg m^{-2})	Grid Station	Year
C. acutus	0.843	0.611	<0.01	1.19	0.40	578.7	600.040	2014
	0.423	0.343	0.04	2.36	0.40	578.7	600.040	2014
	0.439	0.271	0.07	2.28	1.02	336.2	600.040	2014
	0.787	0.646	<0.01	1.27	1.02	336.2	600.040	2014
	0.350	0.414	0.02	2.85	1.56	382.0	610.040	2014
	0.475	0.437	0.01	2.11	0.15	288.2	200.000	2014
	0.345	0.434	0.01	2.90	0.24	233.2	200.-040	2014
	0.563	0.823	<0.01	1.78	0.24	233.2	200.-040	2014
	0.199	0.481	0.01	5.03	-0.10	24.8	100.160	2014
	0.112	0.148	0.19	8.93	-0.10	24.8	100.160	2014
	0.363	0.172	0.21	2.76	1.53	54.9	600.040	2013
	0.164	0.290	0.09	6.11	0.65		600.200	2013
	0.297	0.178	0.26	3.37	1.36	54.6	200.040	2013
	0.105	0.507	0.01	9.52	2.14	142.5	190.-032	2013
	0.249	0.390	0.02	4.02	-0.70	155.2	-127.-019	2013
	0.252	0.534	<0.01	3.98	-0.70	155.2	-127.-019	2013
Mean ± SD =	**0.373 ± 0.215**			**3.78 ± 2.50**				

Copepod species	Gut evacuation rate (k, h^{-1})	r^2	p	Gut passage time (1/k, h)	SST (°C)	Chl *a* (mg m^{-2})	Grid Station	Year
C. propinquus	2.503	0.794	<0.01	0.40	1.02	336.2	600.040	2014
	0.632	0.716	<0.01	1.58	1.02	336.2	600.040	2014
	0.540	0.411	0.03	1.85	1.56	382.0	610.040	2014
	0.871	0.287	0.07	1.15	1.56	382.0	610.040	2014
	1.842	0.728	<0.01	0.54	0.24	233.2	200.-040	2014
	0.307	0.449	0.01	3.26	-0.10	24.8	100.160	2014
	0.326	0.597	<0.01	3.07	-0.10	24.8	100.160	2014
	0.545	0.351	0.04	1.84	1.53	54.9	600.040	2013
	0.878	0.269	0.1	1.14	1.53	54.9	600.040	2013
	0.429	0.487	0.01	2.33	0.65	-	600.200	2013
	0.464	0.917	<0.01	2.16	0.65	-	600.200	2013
	0.567	0.316	0.05	1.76	1.36	54.6	200.040	2013
	0.314	0.143	0.2	3.18	1.36	54.6	200.040	2013
	0.198	0.188	0.14	5.06	2.14	142.5	190.-032	2013
	0.682	0.584	<0.01	1.47	2.14	142.5	190.-032	2013
	0.715	0.470	0.01	1.40	-0.70	155.2	-127.019	2013
	0.367	0.242	0.09	2.72	-0.70	155.2	-127.019	2013
	0.972	0.712	<0.01	1.03	-0.93	108.8	216.-005	2012
	0.215	0.796	<0.01	4.66	-1.15	40.3	-080.077	2012
Mean ± SD =	**0.606 ± 0.574**			**2.30 ± 1.27**				

Copepod species	Gut evacuation rate (k, h^{-1})	r^2	p	Gut passage time (1/k, h)	SST (°C)	Chl *a* (mg m^{-2})	Grid Station	Year
R. gigas	0.543	0.581	0.01	1.84	0.40	578.7	600.040	2014
	0.258	0.301	0.05	3.88	1.02	336.2	600.040	2014
	0.465	0.516	0.01	2.15	1.02	336.2	600.040	2014
	0.348	0.367	0.03	2.88	1.56	382.0	610.040	2014
	0.353	0.520	0.01	2.84	1.56	382.0	610.040	2014
	0.471	0.307	0.10	2.12	0.15	288.2	200.000	2014
	0.543	0.381	0.03	1.84	0.24	233.2	200.-040	2014
	1.125	0.615	<0.01	0.89	0.24	233.2	200.-040	2014
	0.551	0.243	0.12	1.82	-0.10	24.8	100.160	2014
	0.437	0.241	0.13	2.29	1.53	54.9	600.040	2013
	1.282	0.517	0.01	0.78	1.53	54.9	600.040	2013
	0.361	0.478	0.01	2.77	2.14	142.5	190.-032	2013
	0.349	0.615	0.07	2.87	-0.70	155.2	-127.019	2013
	0.396	0.363	0.09	2.53	-0.70	155.2	-127.019	2013
	2.028	0.841	<0.01	0.49	-0.93	108.8	216.-005	2012
Mean ± SD =	**0.634 ± 0.481**			**2.13 ± 0.909**				

Table 3.2. Average individual initial gut content and daily ingestion rates. Data are from January 2012, 2013, and 2014 gut content analyses (n = 4, 247, 522, respectively, for all 4 species combined). Copepod species are: *Calanoides acutus*, *Calanus propinquus, Rhincalanus gigas,* and *Metridia gerlachei.* I = k x G x 24 (see *Section 3.2.1* for explanation of k value applied in calculations). Values are mean ± standard deviation; range in parentheses. n = number of gut content samples per species.

Copepod species	Initial gut content (G) (ng{Chl *a* equiv.} ind.$^{-1}$)	Ingestion Rate (I) (ng{Chl *a* equiv.} ind.$^{-1}$ day^{-1})	*n*
C. acutus	4.3 ± 6.2 (<0.1 - 41.2)	37.4 ± 53.7 (<0.1 - 364)	329
C. propinquus	8.4 ± 10.0 (0.2 - 55.2)	133 ± 208 (2.2 - 1430)	193
R. gigas	10.7 ± 12.3 (<0.1 - 58.6)	133 ± 161 (0.5 - 865)	219
M. gerlachei	1.0 ± 1.0 (<0.1 – 3.2)	24.0 ± 23.1 (2.1 – 76.4)	31

Table 3.3. Total abundance (0- 300 m integrated), daily integrated grazing rates, grazing contribution and grazing impact of herbivorous copepods in the WAP calculated from abundance of each species in January of 1993-2013 (n = 202; Chapter 2). Copepod species are: *Calanoides acutus*, *Calanus propinquus, Rhincalanus gigas,* and *Metridia gerlachei,* Clausocalanidae, and *Oithona* sp. Grazing impact is presented as a percentage of phytoplankton biomass (% Chl *a*) and primary productivity (% PP) consumed per day. Values are mean ± standard deviation, with range in parentheses, for the 21-yr time series (n = 202). The mean ± standard deviation and range of phytoplankton biomass (chl *a*) integrated 0-100 m and primary productivity (PP) integrated to the bottom of the photic zone in January 1993-2013 were: Chl *a* (mg m^{-2}) = 84.0 ± 112.9 (12.8 – 1009.5), PP (g C m^{-2} day^{-1}) = 1.18 ± 1.65 (0.04 – 13.88). *Mean includes one station (-100.000 in 2011) with an abundance of (44,378 ind. m^{-2}), over three times the second highest *Calanoides acutus* abundance.

Copepod species	Abundance (ind. m^{-2})	Daily integrated grazing rates ($\mu g\{Chl\text{-}a\ equiv.\}\ m^{-2}\ day^{-1}$)	Daily integrated grazing rates (mg C m^{-2} day^{-1})	Grazing contribution (%)	Grazing impact % Chl a	Grazing impact % PP
*C. acutus**	638 ± 3337 (<1 - 44378)	14.3 ± 118.0 (<0.1 - 1459.0)	0.92 ± 7.43 (<0.1 - 91.92)	7.8 ± 12.6 (0.3 - 88.6)	<0.01 ± 0.04 (0 - 0.57)	0.07 ± 0.38 (0 - 4.68)
C. propinquus	12 ± 37 (0 - 376)	1.7 ± 9.5 (0 - 122.9)	0.11 ± 0.60 (0 - 7.72)	3.3 ± 7.6 (0 - 67.8)	<0.01 ± <0.01 (0 - 0.05)	0.01 ± 0.03 (0 - 0.39)
R. gigas	36 ± 76 (0 - 727)	2.2 ± 3.8 (0 - 25.1)	0.12 ± 0.24 (0 - 1.58)	9.0 ± 12.3 (0 - 70.2)	<0.01 ± 0.01 (0 - 0.19)	0.04 ± 0.10 (0 - 1.01)
M. gerlachei	622 ± 799 (<1 - 5281)	15.1 ± 19.3 (<0.1 - 126.7)	0.95 ± 1.22 (<0.1 - 7.98)	43.2 ± 24.8 (1.4 - 95.9)	0.03 ± 0.03 (0 - 0.19)	0.19 ± 0.34 (0 - 2.27)
Clausocalanidae	228 ± 456 (<1 - 3349)	8.8 ± 17.7 (<0.1 - 127.3)	0.55 ± 1.11 (<0.1 - 8.02)	22.5 ± 15.7 (0.2 - 89.4)	0.02 ± 0.06 (0 - 0.50)	0.18 ± 0.71 (0 - 8.04)
Oithona sp.	482 ± 1306 (0 - 14584)	7.4 ± 20.1 (0 - 218.8)	0.47 ± 1.26 (0 - 13.78)	14.2 ± 13.7 (0 - 75.6)	0.02 ± 0.06 (0 - 0.48)	0.16 ± 0.56 (0 - 5.82)
Total	2019 ± 4481 (13 - 53550)	49.3 ± 145.8 (0.3 - 1782.6)	3.10 ± 9.18 (<0.1 - 112.31)		0.08 ± 0.14 (<0.1 - 1.06)	0.65 ± 1.49 (0.3 - 11.39)

Table 3.4. Daily copepod egestion rates and fecal pellet C:N ratios. Location corresponds to where experiments were conducted ("North, Coast" is near Anvers Is., "South, Coast" is near Avian Is.). 'Initial chl *a*' is the average concentration of chl *a* in fecatrons (n = 3) at the start of the experiment. 'Station chl *a*' refers to integrated (100 m) chl *a* at the station where copepods were collected. Results are shown for *Calanoides acutus*, *Calanus propinquus, Rhincalanus gigas,* and *Paraeuchaeta antarctica.* "All" = mean for all locations combined, range in parentheses. Values are mean ± standard deviation; [n] = number of fecatrons. All experiments were performed in January in given year.

Year	Location	Initial Chl *a* (ug^{-1})	Station Chl *a* ($mg\ m^{-2}$)	SST (°C)	Egestion Rate (µg C $ind.^{-1}$ day^{-1})				Fecal pellet C:N (µg C:µg N)			
					C. propinquus	*R. gigas*	*C. acutus*	*P. antarctica*	*C. propinquus*	*R. gigas*	*C. acutus*	*P. antarctica*
2013	North, Coast	1.69	54.9	0.56	7.45 ± 2.45 [3]	3.03 ± 0.40 [3]	-	11.6 ± 7.39 [2]	12.6 ± 4.70 [3]	5.56 ± 1.27 [2]	-	8.05 ± 3.02 [2]
2013	South, Coast	1.34	142.5	1.98	6.91 ± 2.01 [2]	2.58 ± 1.36 [2]	6.46 [1]	17.9 ± 16.8 [3]	5.26 ± 2.22 [2]	3.86 ± 1.50 [2]	9.68 [1]	6.95 ± 2.54 [3]
2014	North, Coast	0.59	578.7	1.57	24.20 [1]	5.60 ± 5.14 [4]	4.84 ± 1.95 [4]		12.6 [1]	5.08 ± 1.32 [4]	7.14 ± 1.81 [4]	-
2014	North, Coast	0.25	336.2	1.13	3.28 ± 1.67 [5]	1.37 ± 0.59 [4]	0.89 ± 0.10 [2]		3.06 ± 0.96 [5]	4.07 ± 2.15 [4]	4.21 ± 0.19 [2]	
2014	South, Coast	1.50	233.2	0.48	-	1.68 ± 0.93 [3]	3.16 ± 2.11 [4]	-	-	22.5 ± 9.94 [3]	6.18 ± 1.72 [4]	
All	All				6.98 ± 6.27 (1.26 - 24.2)	2.95 ± 2.91 (0.60 - 13.2)	3.66 ± 2.33 (0.82 - 7.69)	15.4 ± 12.9 (6.36 - 37.3)	6.94 ± 5.13 (1.71 - 17.7)	8.20 ± 8.43 (1.73 - 28.5)	6.49 ± 2.0 (4.07 - 9.68)	7.39 ± 2.42 (5.03 - 10.2)

Table 3.5. Total abundance (0- 300 m integrated) and daily integrated egestion rates of *Calanoides acutus*, *Calanus propinquus, Rhincalanus gigas,* and *Paraeuchaeta antarctica.* Abundance is from stations sampled in January 1993-2013 (n = 202; Chapter 2). Total integrated egestion is the product of mean egestion rate for each species (see Table 3.4) and integrated abundance (ind. m^{-2}) from tows collected in January 1993 – 2013 (n = 202). Values are mean ± standard deviation; range in parentheses. *Mean includes one station (-100.000 in 2011) with an abundance of (44,378 ind. m^{-2}), over three times the next highest *Calanoides acutus* abundance.

		Daily integrated egestion rates
Taxon	Abundance (ind. m^{-2})	(mg C m^{-2} day^{-1})
*C. acutus**	638 ± 3337	2.34 ± 12.21
	(<1 - 44378)	(<0.01 - 162.35)
C. propinquus	12 ± 37	0.09 ± 0.25
	(0 - 376)	(0 - 2.62)
R. gigas	36 ± 76	0.11 ± 0.22
	(0 - 727)	(0 - 2.14)
P. antarctica	622 ± 799	0.02 ± 0.04
	(<1 - 5281)	(0 - 0.42)
Total	2019 ± 4481	2.54 ± 12.41
	(13 - 53550)	(<0.01 - 165.07)

Table 3.6. Individual copepod elemental composition and daily rations. Copepods for elemental composition were collected in January 2013 and 2014; differences carbon content, dry weight, C:N and % carbon (proportion of dry weight that is carbon) among species are significant ($p < 0.001$, 1-way ANOVA). Values are mean ± standard deviation; n = number of animals analyzed. Individual copepod daily rations expressed as a percentage of body carbon ingested or egested daily. Copepod species are: *Calanoides acutus*, *Calanus propinquus*, *Rhincalanus gigas*, and *Paraeuchaeta antarctica*. We did not include ingestion for *P. antarctica*, because it is a carnivorous copepod and we did not conduct ingestion experiments. Average ingestion and egestion rate for each species are listed for comparison. Values are mean; range in parentheses.

	C. acutus	*C. propinquus*	*R. gigas*	*P. antarctica*
Copepod elemental composition				
mgC	0.37 ± 0.14	0.67 ± 0.19	0.42 ± 0.18	2.13 ± 0.76
Dry Wt. (mg)	0.83 ± 0.40	1.53 ± 0.32	1.27 ± 0.36	4.41 ± 1.45
% Carbon	47.8 ± 14.9	44.3 ± 12.5	32.8 ± 8.25	48.1 ± 2.85
C:N (µg C:µg N)	7.30 ± 1.84	5.07 ± 1.49	4.71 ± 1.25	7.66 ± 1.44
n	24	21	24	10
Copepod daily ingestion				
Ingestion Rate (ug C ind.$^{-1}$ day^{-1})	2.36 (0 - 22.9)	8.36 (<0.1 - 90.1)	8.4 (<0.1 - 54.5)	
Body Ration (% C ingested ind.$^{-1}$ day^{-1})	0.64 (0 - 6.3)	1.25 (<0.1 - 13.5)	1.99 (<0.1 - 12.9)	
Copepod daily egestion				
Egestion Rate (ug C ind.$^{-1}$ day^{-1})	3.66 (0.8 - 7.7)	6.98 (1.3 - 24.2)	2.95 (0.6 - 13.3)	15.4 (6.4 - 37.3)
Body Ration (% C egested ind.$^{-1}$ day^{-1})	1.08 (0.27 – 2.03)	0.89 (0.45 – 2.02)	1.58 (0.33 – 3.21)	0.69 (0.50 – 0.84)

Table 3.7. Literature values of gut evacuation (k) and daily ingestion rates for dominant copepods in different regions of the Southern Ocean: *Calanoides acutus*, *Calanus propinquus, Rhincalanus gigas, Metridia gerlachei, Clausocalanus* sp., and *Oithona* spp. Values presented are calculated using the gut fluorescence technique, and ingestion rates are de-corrected for pigment destruction (if necessary). Values from the present study (bolded) are included for comparison.

[a] Dubischar and Bathmann (1997)

[b] Tirelli and Mayzaud (1999)

[c] Li et al. (2001)

[d] Froneman et al. (2000)

[e] Pakhomov and Froneman (2004a)

[f] Atkinson et al. (1992)

[g] Perissinotto (1992)

[h] Bernard and Froneman (2003)

[i] Bernard and Froneman (2005)

[j] Atkinson (1996)

Copepod species	Gut evacuation rate (k) (h^{-1})	Ingestion rate (I) [ng(Chl *a* equiv.)ind.$^{-1}$day^{-1}]	Region	Season	Reference
C. acutus	**0.4 (0.1-0.8)**	**37 (<1-364)**	**Western Antarctic Peninsula**	**Summer**	**This study**
	0.7-1.0	28-60	APF of the Lazarev Sea; Seasonal Ice Zone of the Indian Sector	Spring	a,b
	0.8	50-83	Prydz Bay (pack-ice)	Summer	c
	1.2-1.9	34-51	APF; Spring Ice Edge & Marginal Ice Zone of the Lazarev Sea	Summer	d,e
	1.7	326	Prydz Bay (polynya)	Summer	c
	2.1-5.1	82-775	South Georgia	Summer	f
	2.8		Winter Ice Edge of the Lazarev Sea	Summer	d
C. propinquus	**0.7 (0.2-2.5)**	**133 (2-1429)**	**Western Antarctic Peninsula**	**Summer**	**This study**
	0.2-3.2	3-461	Spring & Winter Ice Edge of the Lazarev Sea; Seasonal Ice Zone of the Indian Sector	Spring	a,b
	0.9-2.7	75-205	Spring & Winter Ice Edge of the Lazarev Sea	Summer	d,e
R. gigas	**0.6 (0.3 - 2.0)**	**133 (<1-865)**	**Western Antarctic Peninsula**	**Summer**	**This study**
	0.3-1.0	21-230	APF of the Lazarev Sea; Seasonal Ice Zone of the Indian Sector	Spring	a,b
	.5-1.7	182-549	South Georgia	Summer	f
	0.5-2.9	46-145	APF; Spring Ice Edge & Marginal Ice Zone of the Lazarev Sea	Summer	d,e
M. gerlachei	**1.0***	**24 (2-76)**	**Western Antarctic Peninsula**	**Summer**	**This study**
	0.4-1.8	26-95	Marginal Ice Zone, Spring & Winter Ice Edge of the Lazarev Sea	Summer	d,e
	0.6 - 0.7	13-132	Prydz Bay	Summer	c
	1.75		Prince Edward Archipelago	Autumn	g
Clausocalanidae	0.4	39-285	APF near Prince Edward Islands	Autumn	h,i
	0.9		South Georgia	Summer	j
	1.41		Prince Edward Archipelago	Autumn	g
		76	Spring Ice Edge of the Lazarev Sea	Summer	e
Oithona spp.	0.4-0.6	16-111	APF near Prince Edward Islands	Autumn	h,i
	1.5		South Georgia	Summer	j
		16	Spring Ice Edge of the Lazarev Sea	Summer	e

Table 3.8. Comparison of individual daily body ration (% carbon) ingested as phytoplankton for dominant copepods in different regions of the Southern Ocean. Copepods are: *Calanoides acutus*, *Calanus propinquus, Rhincalanus gigas, Metridia gerlachei, Oithona* spp. Values from the present study are in bold.

Copepod species	Body Ration (%C ingested ind.$^{-1}$ day^{-1})	Region	Season	Reference
C. acutus	**0.6 (<0.1 - 6.2)**	**Western Antarctic Peninsula**	**Summer**	**This study**
	0.2 – 1.1	Amundsen Sea	Summer	[a]
	0 - 7	Gerlache & Bellingshausen Sea	Summer	[b,c]
	5.6 - 27	South Georgia	Summer	[d]
	3.2 – 28.0	Antarctic Peninsula	Summer	[e]
C. propinquus	**1.3 (<0.1 - 13.5)**	**Western Antarctic Peninsula**	**Summer**	**This study**
	0 - 15	Bellinghausen Sea	Summer	[b,f]
	5.3 – 23.1	Antarctic Peninsula	Summer	[e]
R. gigas	**2.0 (<0.1 - 12.9)**	**Western Antarctic Peninsula**	**Summer**	**This study**
	0.1 – 0.3	Amundsen Sea	Summer	[a]
	0.8 - 2.8	Bellinghausen Sea	Summer	[b]
	1.5 - 3.0	South Georgia	Summer	[d,g]
	1.3 – 9.6	Antarctic Peninsula	Summer	[e]
M. gerlachei	0.5 - 10.4	Bellinghausen and Amundsen Sea	Summer	[a,b,f]
	6.4 – 35.2	Antarctic Peninsula	Summer	[e]
Oithona sp.	0.5 - 3.5	Bellinghausen Sea	Summer	[b]

[a]Lee et al. (2013)
[b]Atkinson & Shreeve (1995)
[c]Calbet et al. (2006)
[d]Atkinson et al. (1992)
[e]Schnack (1985)
[f]Metz and Schnck-Schiel (1995)
[g]Atkinson et al. (1996a)

Table 3.9. Literature values for daily individual egestion rate and integrated egestion rates for copepods, and other mesozooplankton at high latitudes. Values from the present study (bolded) are included for comparison.

Taxon	Egestion Rate ($\mu g\ C\ ind.^{-1}\ day^{-1}$)	Daily Integrated Egestion ($mg\ C\ m^{-2}\ day^{-1}$)	Region	Reference
Copepods	**5.5 (0.9 – 24.2)**	**2.5 (0 – 165)**	**Western Antarctic Peninsula**	**This study**
	0.2 – 0.8	-	Antarctic Polar Front at 170°W	[a]
	0.4 – 3.8	-	Norwegian Shelf	[b]
	0.9 – 9.3	20 – 60	Barents Sea	[c]
	1.7	0.4 – 1.7	Central Arctic	[d]
	-	44 – 122	Baffin Bay	[e]
	-	0.2 - 20	Southern Indian Ocean	[f]
Mesozooplankton	-	0.2 – 0.6	ACC and APF of the Lazarev Sea	[g]
	-	12.4	Marginal Ice Zone of the Lazarev Sea	[g]
Krill	0 - 745	-	South Georgia	[h]
Salp blooms	-	20	Antarctic Peninsula	[i]

[a]Dagg et al. (2003)
[b]Urban-Rich et al. (1999)
[c]Wexels Riser et al. (2007)
[d]Olli et al. (2007)
[e]Sampei et al. (2004)
[f]Møller et al. (2011)
[g]Dubischar and Bathmann (2002)
[h]Atkinson et al. (2012a)
[i]Phillips et al. (2009)

Figure 3.1. Stations sampled during January 2012, 2013 and 2014 off the Western Antarctic Peninsula. Black stars indicate 'process study' sites where gut evacuation rate (GER) experiments, gut content (GC) samples collected, and fecal pellet production (FPP) experiments were conducted in 2013 and 2014. Additional locations of GER experiment and GC sample collection in 2012, 2013, and 2014 are indicated (see Legend). Study region, highlighted by box, in relation to Antarctic continent (inset). AN: Anvers Island, AD: Adelaide Island, MB: Marguerite Bay, C: Charcot Island. Palmer Station is located on Anvers Island. LTER grid lines are numbered (600 to -100). Solid lines separate the 'north' and 'south' gradients. Coast, shelf, and slope regions are separated by a dashed line. All region divisions are based on hydrographic and sea-ice conditions (Martinson et al., 2008; Stammerjohn et al., 2008a).

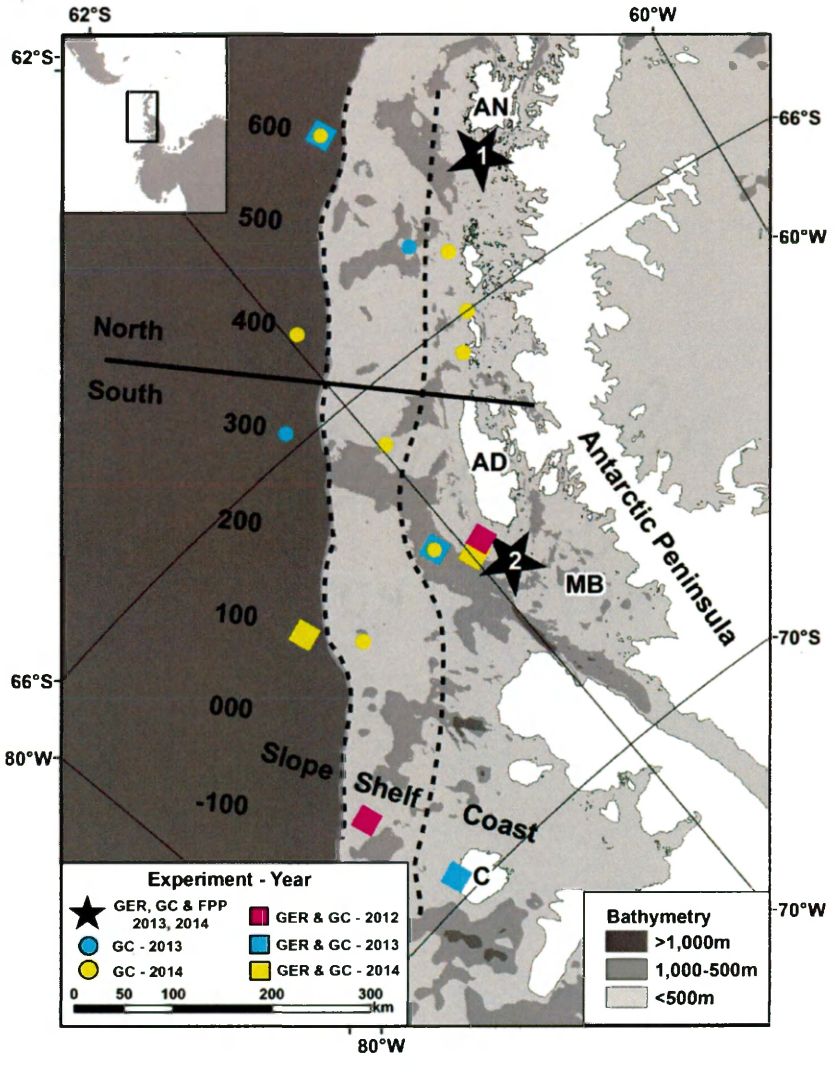
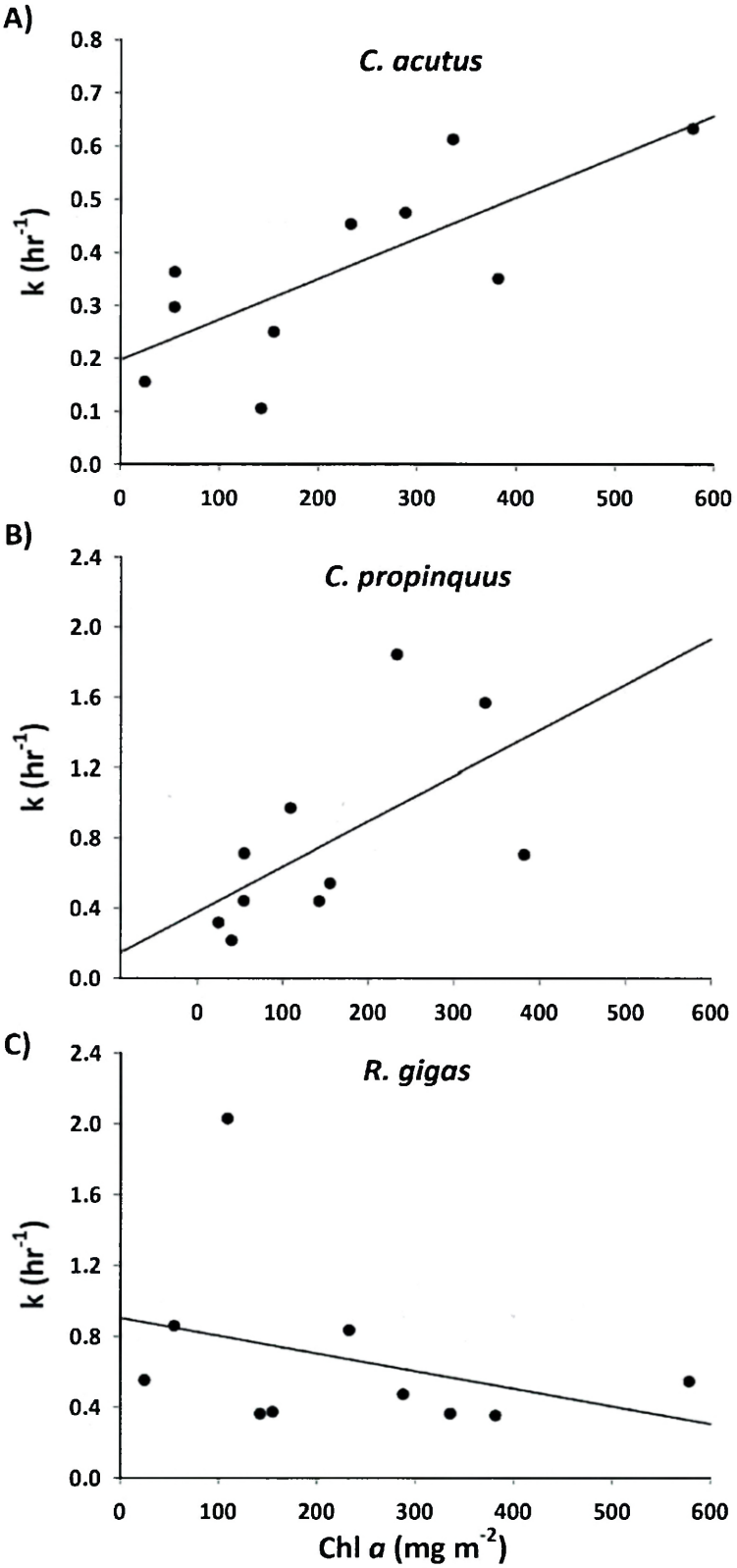

62°S
60°W
62°S
66°S
60°W
AN
1
600
500
North
400
South
300
AD
Antarctic Peninsula
200
2
MB
100
70°S
66°S
000
80°W
Slope
Shelf
Coast
-100
C
70°W
Experiment - Year
GER, GC & FPP 2013, 2014
GC - 2013
GC - 2014
GER & GC - 2012
GER & GC - 2013
GER & GC - 2014
0 50 100 200 300 km
Bathymetry
>1,000m
1,000-500m
<500m
80°W

Figure 3.2. Relationship between integrated (0-100 m) chl *a* and copepod gut evacuation rate constants (k, hr^{-1}). Experiments were conducted in January 2012, 2013, and 2014 with: A) *Calanoides acutus* ($k = [7.65e^{-4} * chl\ a] + 0.197$, $r^2 = 0.57$, $p = 0.011$, $n = 10$), B) *Calanus propinquus* ($k = [2.59e^{-3} * chl\ a] + 0.378$, $r^2 = 0.37$, $p = 0.05$, $n = 10$), and C) *Rhincalanus gigas* ($k = -[1.00e^{-3} * chl\ a] + 0.904$, $r^2 = 0.11$, $p = 0.348$, $n = 10$). k values (hr^{-1}) are an average from replicate experiments (if available) at each location.


A)
C. acutus
k (hr-1)
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0
100
200
300
400
500
600
B)
C. propinquus
k (hr-1)
0.0
0.4
0.8
1.2
1.6
2.0
2.4
0
100
200
300
400
500
600
C)
R. gigas
k (hr-1)
0.0
0.4
0.8
1.2
1.6
2.0
2.4
0
100
200
300
400
500
600
Chl a (mg m-2)

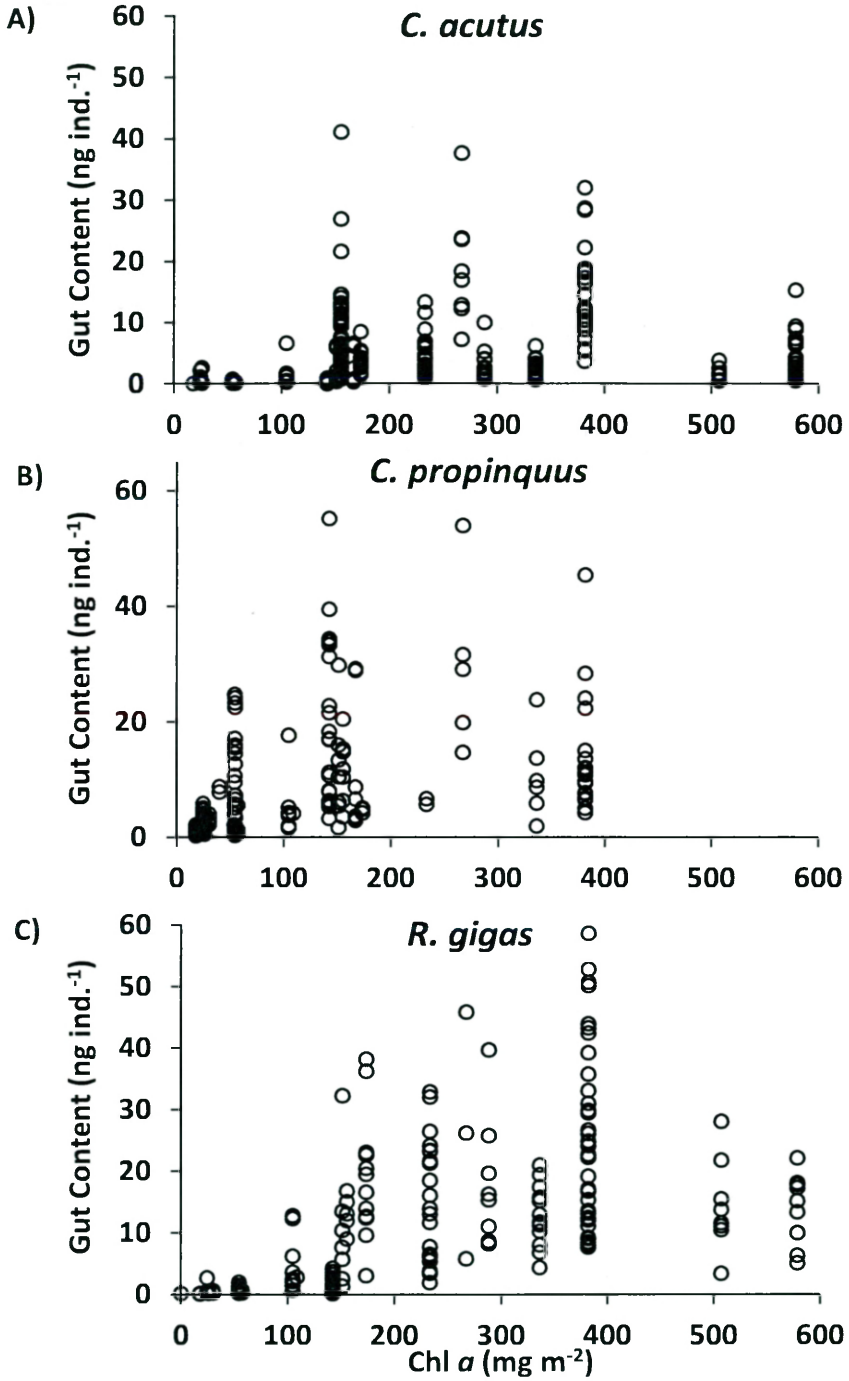


Figure 3.3. Variation in individual copepod gut content with chl *a* for A) *Calanoides acutus* (n = 321), B) *Calanus propinquus* (n = 176), and C) *Rhincalanus gigas* (n = 219). Chl *a* integrated to 0-100 m.

Figure 3.4. Relationship between integrated (0-100 m) chl *a* and copepod daily ingestion rates (I). A) *Calanoides acutus* (I = [0.130 * chl *a*] – 0.658, $r^2 = 0.48$, $p = 0.001$, $n = 21$), B) *Calanus propinquus* (I = [1.27 * chl *a*] – 2.06, $r^2 = 0.55$, $p < 0.001$, $n = 22$), C) *Rhincalanus gigas* (I = [0.478 * chl *a*) + 28.4, $r^2 = 0.41$, $p < 0.001$, $n = 22$). Ingestion rates are an average of replicates at each location ($n = 1 – 53$).

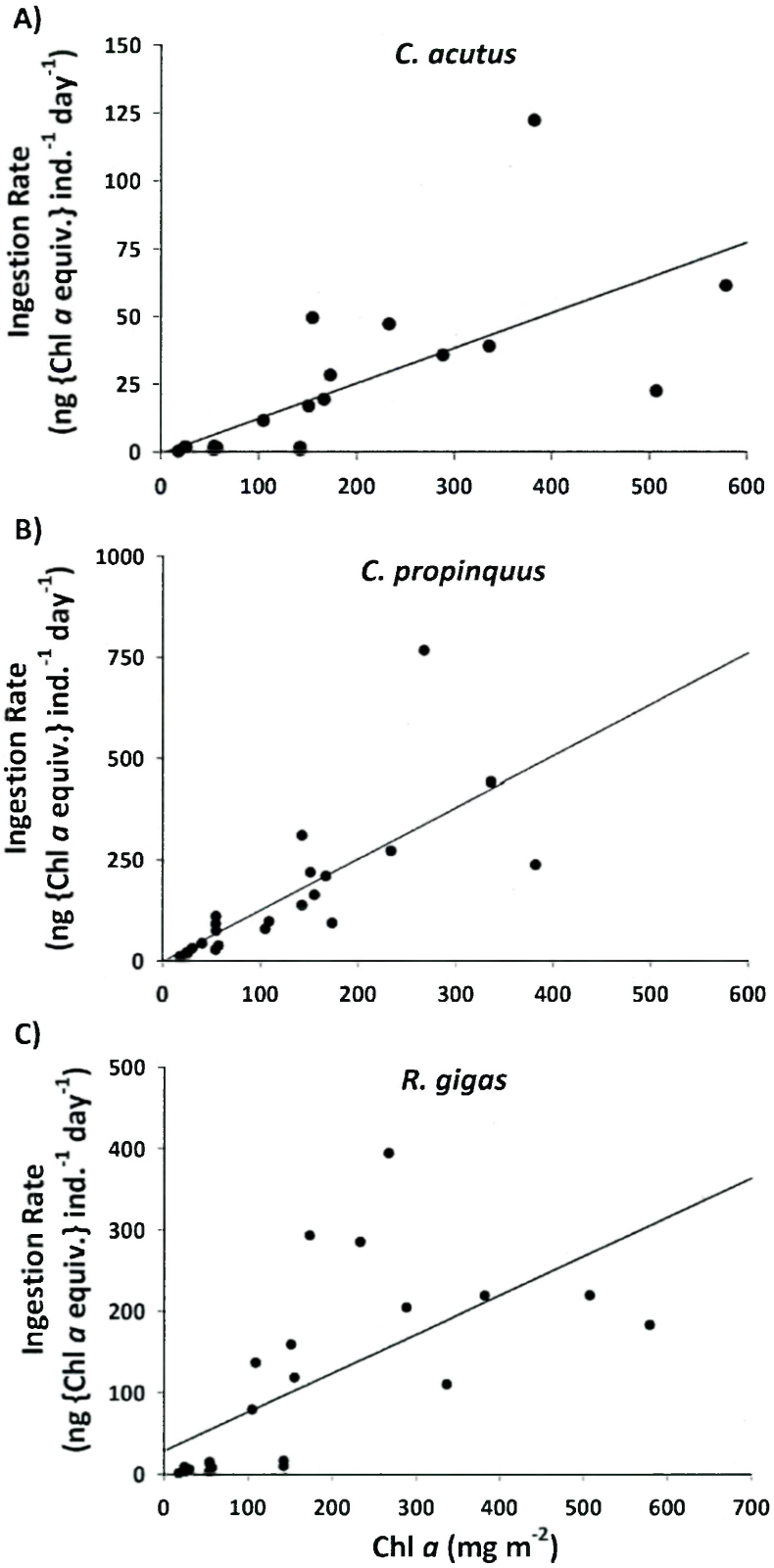

A)
C. acutus
Ingestion Rate
(ng {Chl a equiv.} ind.-1 day-1)
150
125
100
75
50
25
0
0
100
200
300
400
500
600
B)
C. propinquus
Ingestion Rate
(ng {Chl a equiv.} ind.-1 day-1)
1000
750
500
250
0
0
100
200
300
400
500
600
C)
R. gigas
Ingestion Rate
(ng {Chl a equiv.} ind.-1 day-1)
500
400
300
200
100
0
0
100
200
300
400
500
600
700
Chl a (mg m-2)

Figure 3.5. Regional comparison of water column chl *a* and copepod grazing parameters from experiments conducted in January 2012, 2013, and 2014. A) chl *a* integrated 0-100 m; B) gut evacuation rate constant, C) initial gut content, and D) daily ingestion rate for the copepods *Calanoides acutus, Calanus propinquus*, and *Rhincalanus gigas*. Error bars are standard error, letters indicate statistically significant ($p < 0.001$, 2-way ANOVA) differences in grazing parameters among regions for each species (lower case, a > b > c) or all for species combined (upper case, A > B > C). Regions designated with the same letter, or no letter, are not significantly different ($p > 0.05$). Significant difference in chl *a* between regions is labeled as described above; there are no significant differences in gut evacuation rates between regions for any species. † indicates a significant difference between species within the same region ($p < 0.05$, 1-way ANOVA), and species significantly different from each other within a region are indicated with a different number (x > y). Open circle indicates no experiment for species at that location.

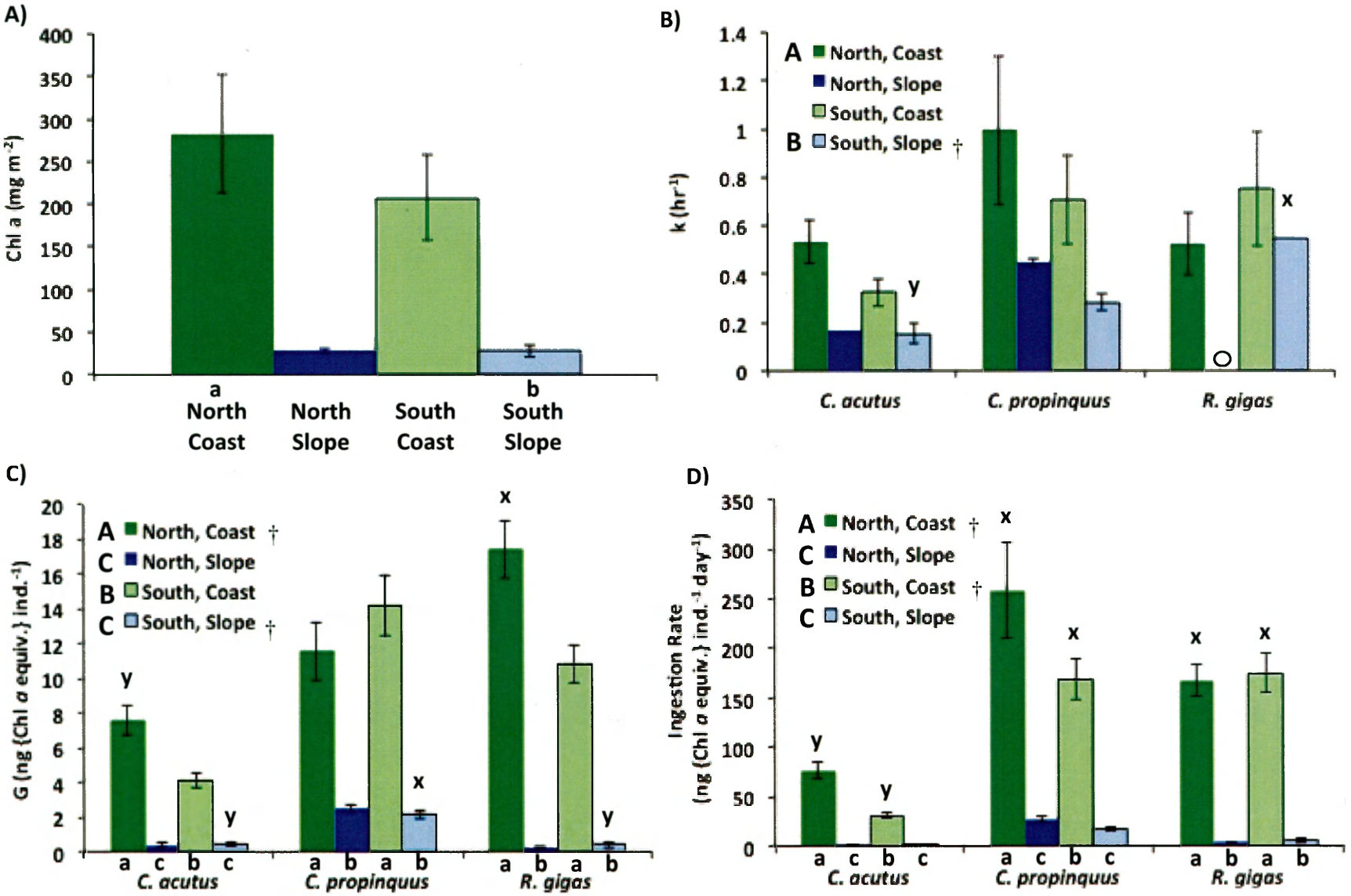
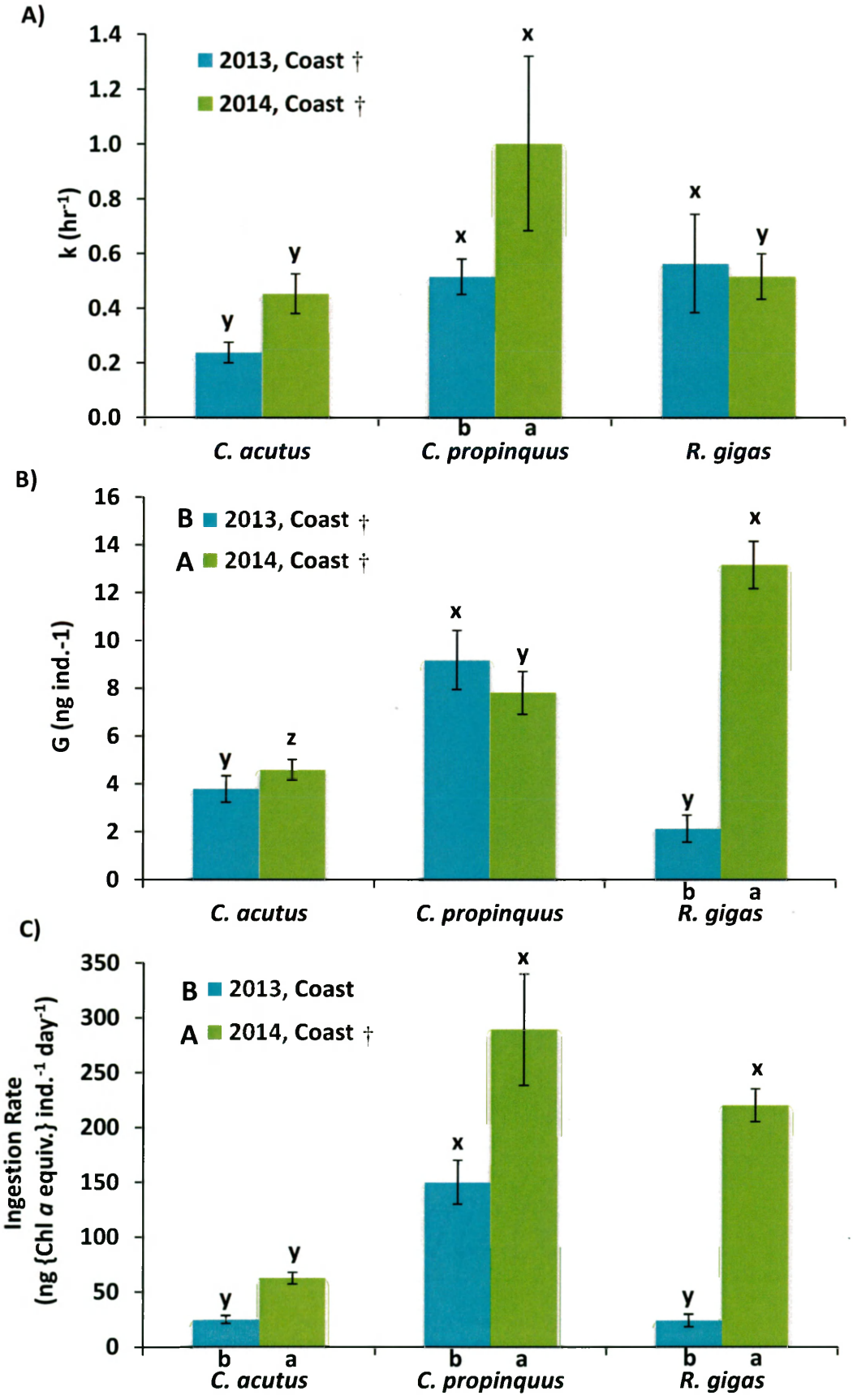

A)
Chl a (mg m-2)
400
350
300
250
200
150
100
50
0
a
b
North Coast
North Slope
South Coast
South Slope
B)
k (hr-1)
1.4
1.2
1
0.8
0.6
0.4
0.2
0
A North, Coast
North, Slope
South, Coast
B South, Slope †
y
x
C. acutus
C. propinquus
R. gigas
C)
G (ng {Chl a equiv.} ind.-1)
20
18
16
14
12
10
8
6
4
2
0
A North, Coast †
C North, Slope
B South, Coast
C South, Slope †
a c b c
a b a b
a b a b
C. acutus
C. propinquus
R. gigas
D)
Ingestion Rate (ng {Chl a equiv.} ind.-1 day-1)
350
300
250
200
150
100
50
0
A North, Coast †
C North, Slope
B South, Coast †
C South, Slope
a c b c
a c b c
a b a b
C. acutus
C. propinquus
R. gigas

Figure 3.6. Comparison of gut evacuation rates (k), gut content (G), and ingestion rates measured in the coastal region of the WAP in January 2013 (low chl *a* = 92.9 ± 51.3 mg m^{-2}; mean ± standard deviation) and 2014 (high chl *a* bloom = 335 ± 152 mg m^{-2}) for the copepods *Calanoides acutus, Calanus propinquus*, and *Rhincalanus gigas*. Error bars are standard error, labels indicate statistically significant ($p < 0.05$, 2-way ANOVA) differences in ingestion rate between years for each species (or all species combined indicated by capital letters): a > b (A > B). † indicates a significant difference between species in the same year ($p < 0.05$, 1-way ANOVA), and species significantly different from each other within a year are indicated with a different number (x > y > z).


A)
2013, Coast †
2014, Coast †
k (hr-1)
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
y
y
x
x
x
y
b
a
C. acutus
C. propinquus
R. gigas
B)
B 2013, Coast †
A 2014, Coast †
G (ng ind.-1)
16
14
12
10
8
6
4
2
0
y
z
x
y
y
x
b
a
C. acutus
C. propinquus
R. gigas
C)
B 2013, Coast
A 2014, Coast †
Ingestion Rate
(ng {Chl a equiv.} ind.-1 day-1)
350
300
250
200
150
100
50
0
y
y
x
x
y
x
b
a
b
a
b
a
C. acutus
C. propinquus
R. gigas

CHAPTER 4

Summary and Concluding Remarks

Copepods are the dominant mesozooplankton in the Southern Ocean, important grazers on phytoplankton, and contributors to carbon export through production of fecal pellets. Thus a comprehensive understanding of their role in the Western Antarctic Peninsula (WAP) marine food web is essential in understanding the implications of climate change in this region. My research is the first examination of decadal-scale trends in copepod abundance in the Southern Ocean, and of relationships between these long-term trends and environmental variables (Chapter 2). Furthermore, my study represents the most comprehensive picture to date of the role of copepods in grazing and fecal pellet production in the WAP (Chapter 3).

The WAP has some of the highest seasonal productivity in the Southern Ocean, supporting a marine ecosystem with large summer phytoplankton blooms (Ducklow et al. 2012). However, a decrease in seasonal sea ice over the past few decades has led to a latitudinal 'climate gradient', affecting food web dynamics with documented changes at all trophic levels (Montes-Hugo et al. 2008, Stammerjohn, Martinson, Smith, & Iannuzzi 2008, Steinberg, Martinson, et al. 2012). Changes in the abundance and community structure of many macrozooplankton taxa have been documented in the WAP, and these changes have been shown to be correlated sea ice, phytoplankton biomass and productivity, and climate indices (Loeb and Santora, 2012; Loeb et al., 2008; Saba et al., 2014; Steinberg et al., in review). My research is the first to show that copepods are increasing in the WAP. My findings show a significant increase from 1993-2013 with higher abundances in years with earlier sea ice retreat and higher phytoplankton biomass and productivity. This increase may be due to a phenology shift with earlier sea ice retreat allowing for earlier recruitment and potentially increasing copepodite survival

over winter months. Furthermore, increasing copepod abundance may also be linked to the increase in chlorophyll *a*, which likely provided more favorable conditions for copepod growth over the time series (Montes-Hugo et al. 2009).

Copepod impact on grazing of phytoplankton biomass and productivity in the WAP was low (on average <1% chl *a* and 1% PP), but similar to other regions of the Southern Ocean. This confirms results from prior studies indicating that microzooplankton, as opposed to meso- and macrozooplankton, are the dominant grazers of phytoplankton in the WAP (Bernard et al. 2012, Garzio et al. 2013). Ingestion rates were over 10-fold higher during high bloom conditions in the productive coastal region than offshore. Body rations further suggest that copepods grazed predominantly on phytoplankton in higher chl *a* conditions, but relied on other sources of carbon (i.e., microzooplankton, protozoans) when phytoplankton biomass was lower. This study is only the second examination of individual copepod species egestion rates in the Southern Ocean (Dagg et al. 2003). We found high egestion rates, even in lower chl *a* conditions, but with high retention in the upper water column. Thus, at least compared to krill, copepods may not be efficient exporters of C to depth in this region. My grazing and egestion studies included only the large, dominant species. Future studies quantifying grazing impact and egestion of small copepod species and copepodite stages of larger species are necessary to gain a more comprehensive understanding of the flow of carbon and energy through copepods in the WAP (Atkinson & Shreeve 1995, Fransz & Gonzalez 1995, Atkinson 1996).

Copepod abundances appear to be increasing over time and they may in the future exert higher grazing pressure on phytoplankton, microzooplankton, and other smaller

metazoans. Further studies exploring copepod feeding on microzooplankton, particularly ciliates and other abundant protists, are needed (Garzio & Steinberg 2013, Garzio et al. 2013), to test our hypothesis that a significant proportion of copepod diet is derived from ingestion of non-phytoplankton prey. Furthermore, copepods are also an important component in the diet of many macrozooplankton (Atkinson & Snyder 1997, Froneman & Pakhomov 1998, Kruse et al. 2010) and more research is needed on the importance of top-down control on copepods in the WAP.

While our results suggest an increase in abundance across all dominant copepod taxa, their future in the WAP is uncertain. Climate change scenarios for the region predict the latitudinal 'climate gradient' will shift pole-ward, resulting in decreased phytoplankton biomass and productivity as earlier sea ice retreat coincides with increased winds and low light conditions (Arrigo & Thomas 2004, Montes-Hugo et al. 2009). Thus, the earlier sea ice retreat and longer ice-free summer season that is currently favorable to copepods may not remain consistent, and environmental conditions could become detrimental for the predominantly herbivorous species with winter diapause (i.e., *C. acutus*; Tarling et al. 2004, Hunt et al. 2011). Further research should examine the physiology of these copepods to understand their tolerance to warmer conditions and how recruitment, development, and diapause might change under this new climate scenario. Finally, the environmental conditions leading to interannual variability of summer copepod abundance in the WAP can be used to predict how the copepods will respond to future environmental changes, and affect flow of carbon through the food web and the export of carbon to depth.

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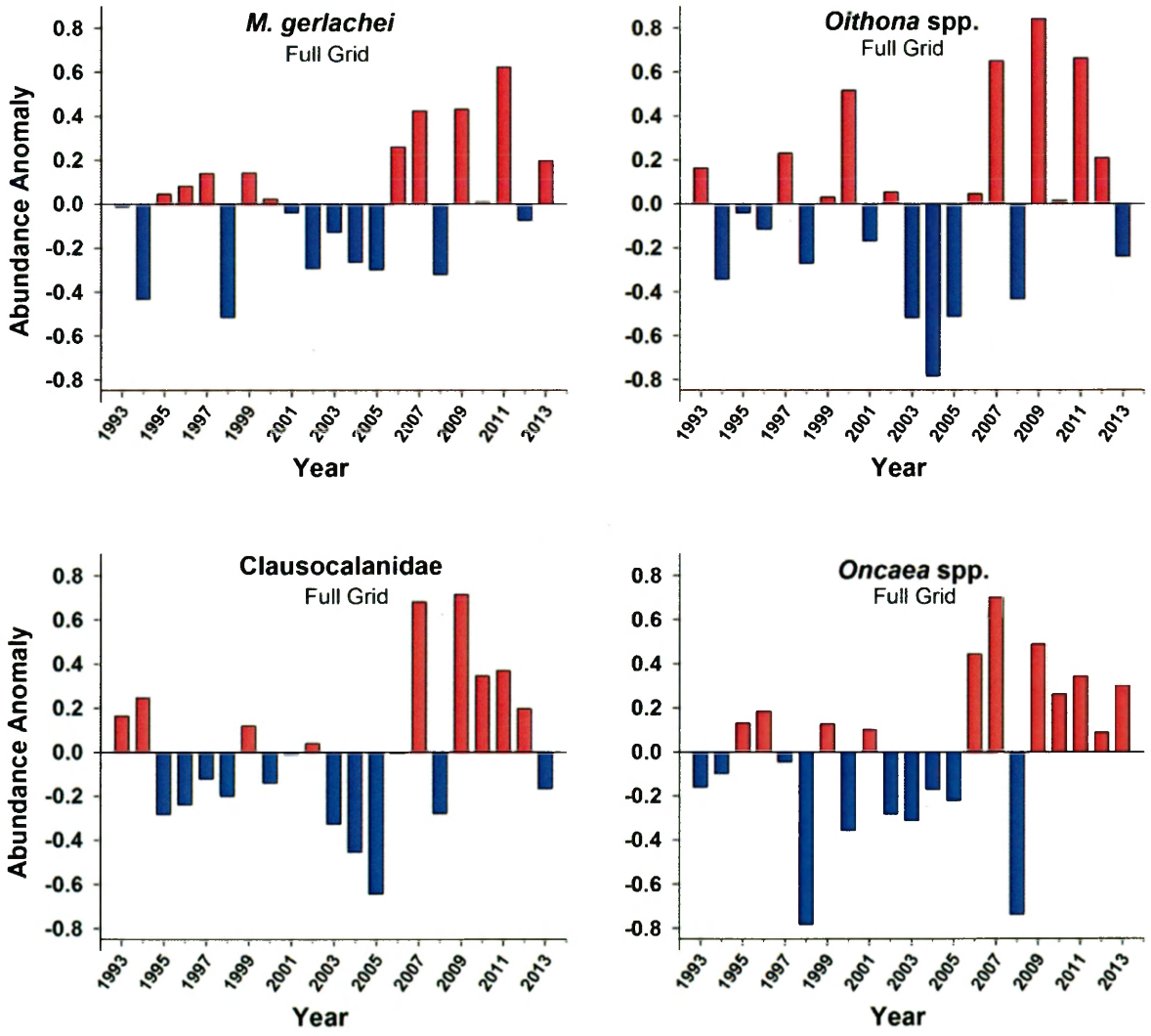
APPENDIX

Appendix 1. Summary of taxa enumerated (at highest taxonomic resolution used). Mean, standard deviation (SD), median, and range of abundance (ind. 1000 m^{-3}). n = 201. Copepods identified as belonging to the family Clausocalanidae likely include *Clausocalanus laticeps* and *Ctenocalanus citer*, but adult males were absent, making identification difficult, and Clausocalanid-like copepodites comprised the majority of this taxa. '*Amphipoda* other' includes amphipods of uncertain or unknown identification. Crustacean nauplii were present in samples, but not included. Mean abundances exclude one outlier tow with a total copepod abundance of $1.8x10^5$ ind. $1000m^{-3}$. Note - *E. superba* juveniles and adults, and salps are not included in counts.

	Abundance (ind. 1000m^{-3})		
	Mean ± SD	**Median**	**Range**
Copepods	**7001 ± 9238**	**3990**	**57 - 67462**
Metridia gerlachei	1996 ± 2434	1140	1 - 15966
Oithona spp.	1570 ± 4330	371	0 - 48615
Calanoides acutus	1402 ± 4186	352	3 - 42646
Clausocalanidae	751 ± 1518	286	2 - 11165
Paraeuchaeta antarctica	664 ± 731	417	0 - 3965
Oncaea spp.	159 ± 324	34	0 - 2254
Rhincalanus gigas	122 ± 254	49	0 - 2423
Farrania frigida	72 ± 127	25	0 - 937
Heterorhabdus spp.	53 ± 95	18	0 - 844
Scolecithricella minor	51 ± 91	24	0 - 945
Calanus propinquus	35 ± 87	10	0 - 791
Haloptilus spp.	23 ± 41	7	0 - 304
Gaetanus tenuispinus	11 ± 35	0	0 - 364
Aetideidae	5 ± 15	0	0 - 148
Candacia sp.	2 ± 17	0	0 - 234
Euchirella sp.	1 ± 5	0	0 - 62
Pleuromamma robusta	1 ± 2	0	0 - 17
Chaetoganths	**524 ± 618**	**302**	**3 - 4452**
Sagitta sp.	522 ± 617	301	3 - 4452
Pseudosagitta sp.	2 ± 6	1	0 - 57
Euphausiids - larvae	**461 ± 1627**	**30**	**0 - 12455**
Euphausiacea (calyptopis)	248 ± 923	22	0 - 9373
Euphausiacea (furcilia)	251 ± 1173	0	0 - 12455
Fish	3 ± 11	**0**	**0 - 97**
Teleostei (larvae)	2 ± 11	0	0 - 97
Channichthyidae	<0.1 ± 0.1	0	0 - 1

	Abundance (ind. 1000m^{-3})		
	Mean ± SD	**Median**	**Range**
Polychaetes	**154 ± 369**	**40**	**0 - 3506**
Polychaeta	139 ± 285	40	0 - 1867
Tomopteris spp. - adult	0.1 ± 0.3	0	0 - 2
Alciopidae	<0.1 ± 0.2	0	0 - 2
Polychaeta (larvae)	14 ± 197	0	0 - 2796
Pteropods	36 ± 71	**14**	**0 - 822**
Limacina helicina antarctica	28 ± 51	7	0 - 455
Clione antarctica	8 ± 29	0.5	0 - 367
Clio pyramidata	<0.1 ± 0.1	0	0 - 1
Amphipods	**35 ± 48**	**19**	**0 - 375**
Primno macropa	23 ± 35	9	0 - 237
Themisto gaudichaudi	3 ± 6	0	0 - 41
Cyllopus sp.	0.2 ± 0.9	0	0 - 11
Gammaridea	0.2 ± 1.7	0	0 - 17
Hyperoche sp.	0.4 ± 1.6	0	0 - 17
Vibilia sp.	1 ± 3	0	0 - 18
Scina sp.	0.1 ± 0.8	0	0 - 10
Amphipoda other	3 ± 9	0	0 - 82
Amphipoda (larvae)	5 ± 30	0	0 - 347
Other			
Ostracoda	333 ± 458	159	0 - 2731
Siphonophorae	57 ± 102	18	0 - 757
Cnidaria	11 ± 62	0	0 - 836
Decapoda	0.3 ± 2.1	0	0 - 28
Cephalopoda	<0.1 ± 0.1	0	0 - 1

Appendix 2. Annual abundance anomaly of the copepods *Metridia gerlachei*, *Oithona* spp., Clausocalanidae, and *Oncaea* spp. for the full grid area.



Appendix 3. Results of stepwise multiple regression analyses addressing the effect of environmental parameters and climate on copepod abundance. Stepwise multiple regression analyses for regional annual mean abundance anomaly for total copepods, and species with the strongest regional trends are shown. Sea ice, primary production, and chl *a* variables are annual anomalies. Explanatory variables and statistical scores obtained from the best model among stepwise multiple regression analyses are shown. Test statistics include r^2 and p-values for the overall model, the coefficient (slope) for the regression equation, the standard error (SE) associated with the model coefficient, the 2 tailed p-value (*p*) used in testing the null hypothesis for each significant model variable, and the partial r^2. n = number of years included in the model.

Copepod	Variable	n	Slope	SE	*p*	*Partial* r^2
Total Copepods	Far North (r^2 = 0.39, *p* = 0.018)	19				
	ME Index (1-yr. lag)		-0.304	0.103	0.010	0.243
	Primary production (0-yr. lag)		0.535	0.268	0.063	0.152
	North (r^2 = 0.53, *p* = 0.004)	21				
	Sea ice retreat (1-yr. lag)		-8.367	2.233	0.002	0.318
	Chl *a* (0-yr. lag)		0.825	0.348	0.030	0.104
	SAM Index (Winter, 1-yr. lag)		0.059	0.030	0.063	0.109
	South (r^2 = 0.64, *p* = <0.001)	19				
	Sea ice retreat (1-yr. lag)		-4.813	1.585	0.008	0.466
	SAM Index (Spring,1-yr. lag)		0.066	0.024	0.015	0.169
	Coast (r^2 = 0.66, *p* = 0.001)	18				
	SAM Index (1-yr. lag)		0.125	0.028	0.001	0.273
	Primary production (1-yr. lag)		0.360	0.114	0.007	0.283
	SAM Index (Autumn,1-yr. lag)		-0.081	0.038	0.052	0.108
	Shelf (r^2 = 0.72, *p* = <0.001)	19				
	Sea ice retreat (1-yr. lag)		-8.782	2.032	0.001	0.438
	Chl *a* (1-yr. lag)		1.001	0.329	0.008	0.173
	Primary production (0-yr. lag)		0.384	0.163	0.032	0.105
	Slope (r^2 = 0.44, *p* = 0.006)	21				
	Sea ice retreat (1-yr. lag)		-11.718	3.241	0.002	0.310
	Chl *a* (0-yr. lag)		1.065	0.522	0.056	0.130
C. acutus	Far North (r^2 = 0.50, *p* = 0.002)	21				
	Sea ice retreat (1-yr. lag)		-6.419	1.941	0.004	0.329
	SAM Index (Winter, 1-yr. lag)		0.065	0.026	0.021	0.175
	North (r^2 = 0.61, *p* = 0.004)	18				
	Primary production (1-yr. lag)		0.386	0.339	0.274	0.319
	Sea ice retreat (1-yr. lag)		-10.735	3.776	0.013	0.170
	SAM Index (Summer, 2-yr. lag)		-0.137	0.067	0.061	0.117
	South (r^2 = 0.54, *p* = <0.001)	19				
	SAM Index (Spring, 1-yr. lag)		0.145	0.032	<0.001	0.543
	Coast (r^2 = 0.62, *p* = <0.001)	21				
	SAM Index (Winter, 1-yr. lag)		0.134	0.034	0.001	0.426
	Sea ice retreat (1-yr. lag)		-8.031	2.634	0.007	0.195
	Shelf (r^2 = 0.35, *p* = 0.005)	21				
	Sea ice retreat (1-yr. lag)		-9.142	2.871	0.005	0.348
	Slope (r^2 = 0.28, *p* = 0.013)	21				
	Sea ice retreat (1-yr. lag)		-13.548	4.955	0.013	0.282

Copepod	Variable	n	Slope	SE	*p*	*Partial* r^2
Clausocalanidae	Far North (r^2 = 0.43, *p* = 0.012)	19				
	Sea ice duration (1-yr. lag)		-2.677	0.850	0.006	0.187
	Primary production (0-yr. lag)		0.794	0.305	0.019	0.241
	North (r^2 = 0.25, *p* = 0.023)	21				
	Sea ice retreat (1-yr. lag)		-8.053	3.245	0.023	0.245
	South (r^2 = 0.57, *p* = <0.001)	19				
	Sea ice days (1-yr. lag)		-3.019	0.632	<0.001	0.573
	Coast (r^2 = 0.26, *p* = 0.018)	21				
	Sea ice retreat (1-yr. lag)		-8.251	3.184	0.018	0.261
	Shelf (r^2 = 0.53, *p* = 0.003)	18				
	Sea ice retreat (1-yr. lag)		-9.671	2.718	0.003	0.470
	Primary production (1-yr. lag)		0.277	0.225	0.237	0.132
	Slope (r^2 = 0.34, *p* = 0.024)	21				
	Sea ice retreat (1-yr. lag)		-11.498	4.051	0.011	0.207
	Chl *a* (0-yr. lag)		1.247	0.653	0.072	0.134
C. propinquus	Far North (r^2 = 0.56, *p* = 0.005)	21				
	ME Index (Autumn, 2-yr. lag)		-0.231	0.058	0.001	0.396
	ME Index (Summer, 2-yr. lag)		0.100	0.049	0.060	0.111
	North (r^2 = 0.74, *p* = <0.001)	18				
	Primary production (1-yr. lag)		0.874	0.174	<0.001	0.417
	ME Index (Summer, 1-yr. lag)		-0.248	0.057	0.001	0.327
	South (r^2 = 0.67, *p* = 0.001)	18				
	Sea ice duration (1-yr. lag)		-2.790	0.687	0.001	0.341
	Primary production (1-yr. lag)		0.503	0.157	0.006	0.203
	SAM Index (Autumn, 1-yr. lag)		0.128	0.054	0.032	0.130
	Coast (r^2 = 0.61, *p* = 0.001)	18				
	Primary production (1-yr. lag)		1.327	0.275	<0.001	0.311
	Chl *a* (1-yr. lag)		-1.331	0.388	0.004	0.303
	Shelf (r^2 = 0.63, *p* = 0.002)	18				
	Primary production (1-yr. lag)		0.801	0.255	0.007	0.252
	Sea ice retreat (2-yr. lag)		-8.836	3.090	0.013	0.171
	SAM Index (Winter, 1-yr. lag)		0.119	0.042	0.014	0.207
	Slope (r^2 = 0.50, *p* = <0.001)	21				
	Sea ice days (1-yr. lag)		-4.570	1.052	<0.001	0.498

Appendix 4. Location, and physical and biological data for grid stations where copepod gut evacuation rate (GER) experiments were conducted and gut content (GC) samples were collected in the Palmer Antarctica Long-Term Ecological Research (PAL LTER) study area in 2012, 2013 and 2014. Grid = PAL LTER station identification (Waters and Smith 1992). Lat = Latitude, Long = Longitude. Temp = water temperature. Chl-*a* = chlorophyll-*a* integrated 0-100m. Copepod species used in GER experiments and collected for GC at each station are listed.

Year	Grid	Lat. (°S)	Long. (°W)	Temp. (°C)	Chl-*a* (mg m^{-2})	Date	Experiments	Copepod Species
2012	216.-005	67.7	69.9	-0.93	108.8	16-Jan	GER, GC	*C. acutus* (GC only), *C. propinquus* (GC only), *R. gigas*
2012	-080.077	68.9	76.3	-1.15	40.3	27-Jan	GER, GC	*C. acutus* (GC only), *C. propinquus, R. gigas* (GC only)
2013	600.040	64.9	64.4	1.53	54.9	06-Jan	GER, GC	*C. acutus, C. propinquus, R. gigas*
2013	609.038	64.9	64.2	0.40	44.2	06-Jan	GC	*C. acutus, C. propinquus, R. gigas*
2013	600.200	64.0	66.9	0.65	-	09-Jan	GER, GC	*C. acutus, C. propinquus, R. gigas* (GC only)
2013	500.100	65.2	66.8	2.77	54.2	09-Jan	GC	*C. acutus, C. propinquus, R. gigas*
2013	300.200	65.9	71.3	0.51	18.1	11-Jan	GC	*C. acutus, C. propinquus, R. gigas*
2013	200.040	67.5	70.6	1.36	54.6	12-Jan	GER, GC	*C. acutus, C. propinquus, R. gigas* (GC only)
2013	190.-032	68.0	69.6	2.14	142.5	16-Jan	GER, GC	*C. acutus, C. propinquus, R. gigas*
2013	-127.-019	69.8	75.8	-0.70	155.2	22-Jan	GER, GC	*C. acutus, C. propinquus, R. gigas*

Year	Grid	Lat. (°S)	Long. (°W)	Temp. (°C)	Chl-*a* (mg m^{-2})	Date	Experiments	Copepod Species
2014	600.040	64.9	64.4	0.40	578.7	07-Jan	GER, GC	*C. acutus, C. propinquus* (GC only), *R. gigas*
2014	610.040	64.9	64.3	1.56	382.0	08-Jan	GER, GC	*C. acutus, C. propinquus, R. gigas*
2014	600.200	64.0	66.9	-0.36	26.0	09-Jan	GC	*C. acutus, C. propinquus, R. gigas, M. gerlachei*
2014	400.200	65.2	69.8	0.83	30.4	12-Jan	GC	*C. propinquus, R. gigas*
2014	300.100	66.5	69.9	-1.51	54.5	12-Jan	GC	*C. acutus, C. propinquus, R. gigas*
2014	200.040	67.5	70.6	0.50	173.4	13-Jan	GC	*C. acutus, C. propinquus, R. gigas, M. gerlachei*
2014	200.000	67.7	69.9	0.15	288.2	14-Jan	GER, GC	*C. acutus, C. propinquus* (GC only), *R. gigas*
2014	200.-040	68.0	69.4	0.24	233.2	15-Jan	GER, GC	*C. acutus, C. propinquus, R. gigas, M. gerlachei* (GC only)
2014	213.-014	67.8	69.5	-0.47	507.3	17-Jan	GC	*C. acutus, R. gigas*
2014	100.100	67.7	73.3	0.12	166.9	21-Jan	GC	*C. acutus, C. propinquus*
2014	100.160	67.3	74.2	-0.10	24.8	21-Jan	GER, GC	*C. acutus, C. propinquus, R. gigas*
2014	500.060	65.5	66.2	0.74	151.2	23-Jan	GC	*C. acutus, C. propinquus, R. gigas, M. gerlachei*
2014	443.035	66.0	66.6	0.96	267.1	23-Jan	GC	*C. acutus, C. propinquus, R. gigas, M. gerlachei*
2014	401.034	65.3	65.2	0.67	104.8	25-Jan	GC	*C. acutus, C. propinquus, R. gigas*
2014	600.040	64.9	64.4	1.02	336.2	27-Jan	GER, GC	*C. acutus, C. propinquus, R. gigas*

Appendix 5. Location, and physical and biological data for grid stations where copepod fecal pellet production (FPP) experiments were conducted in the Palmer Antarctica Long-Term Ecological Research (PAL LTER) study area in 2013, and 2014. Grid = PAL LTER station identification (Waters and Smith 1992). Lat = Latitude, Long = Longitude. Temp = water temperature. Chl-*a* = chlorophyll-*a* integrated 0-100m. Copepod species used in FPP experiments at each station are listed.

Year	Grid	Lat. (°S)	Long. (°W)	Temp. (°C)	Chl-*a* (mg m^{-2})	Date	Copepod Species
2014	600.040	64.9	64.4	1.57	578.7	07-Jan	*C. acutus, C. propinquus, R. gigas*
2014	200.-060	68.1	69.0	0.48	233.2	16-Jan	*C. acutus, R. gigas*
2014	600.040	64.9	64.4	1.13	336.2	27-Jan	*C. acutus, C. propinquus, R. gigas*
2013	619.036	64.8	64.1	0.56	54.9	07-Jan	*C. propinquus, P. antarctica R. gigas*
2013	190.-032	68.0	69.6	1.98	142.5	15-Jan	*C. acutus, C. propinquus, P. antarctica, R. gigas*

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Born in Stevensville, MI on June 2, 1988. Graduated from Lakeshore High School in 2006. Attended James Cook University in Townsville, Australia as an exchange student in 2008. Earned a Bachelor's of Science in Biology and Environmental Science from The College of William and Mary in 2010. Honors thesis investigated the role of zooplankton fecal pellets in carbon flux in the western Antarctic Peninsula. Advisor: Dr. Deborah Steinberg. Employed as a laboratory research assistant for Dr. Deborah Steinberg from 2010 to 2011. Worked as a divemaster in Marbella, Spain in 2011. Entered the Master's of Science program at the Virginia Institute of Marine Science, College of William and Mary under graduate advisor Dr. Deborah Steinberg in 2011.